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Review of the Cloacininae Stossich (Nemata: Strongyloidea) from Australasian marsupials (Marsupialia: Macropodoidea)

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Abstract
The nematode sub-family Cloacininae from Australasian macropodoid marsupials is reviewed. Keys are provided to all genera and species currently known. A revised definition of the sub-family and detailed generic diagnoses are provided. For each species, full synonymies and literature citations are included along with known hosts, geographical distributions and associated DNA sequence data. A brief morphological synopsis of each species is provided together with illustrations of the morphological features needed for identification using the keys. Due to uncertainties relating to the division of the sub-family into tribes, only the nominal allocation to tribe is provided. Two new genera are erected, *Sacculostrongylus* n. gen. for *S. ochetocephalus* (Beveridge, 1986) n. comb., formerly placed within *Monilonema* Beveridge & Johnson, 1981, and *Thylicostrongylus* n. gen., for several species formerly placed in *Wallabinema* Beveridge, 1983.

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Introduction

The strongyloid sub-family Cloacininae Stossich, 1899, currently consisting of some 39 genera and over 300 species, occurs in the stomachs and oesophagi of Australasian macropodoid marsupials. Apart from the diversity of nematode species, which matches or exceeds that found in virtually any other groups of mammals, cloacinine nematodes frequently occur at high intensities of infection, with up to 500,000 being recorded from the stomachs of western grey kangaroos, *Macropus fuliginosus,* by Beveridge & Arundel (1979). Another feature of the sub-family is the occurrence of multiple species in the same individual host, forming so-called 'species flocks' (Beveridge et al., 2002). The greatest morphological diversity is noticed primarily in the labial, buccal and oesophageal structures rather than in the reproductive systems, apart from metrical data such as spicule lengths and the morphology of the vagina.

The taxonomic literature on this sub-family is now extensive but is widely scattered. Most, but not all, of the early descriptions of genera and species have been revisited and supplemented by new material, and host ranges have been better defined. In addition, revisions have uncovered apparent errors in the identification of type and other hosts with numerous corrections having been made (for example see Spratt & Beveridge, 2016). A list of nematode species arranged by host, although slightly dated, is provided in Spratt & Beveridge (2016).

In spite of the relatively large number of species described, it is most unlikely that the full extent of diversity within this nematode subfamily has been uncovered. For example, Beveridge et al. (2014a) listed five undescribed species from the common swamp wallaby, *Wallabia bicolor*, for which insufficient material was available for formal descriptions and Beveridge (2020f) noted the difficulties in obtaining sufficient numbers of small nematode species occurring in the stomachs of other host species at low levels of intensity of infection to enable formal descriptions. Two species of potoroines (*Bettongia lesueur* and *Potorous gilberti*) as well as six species of macropodines (*Dendrolagus spadix*, *D. ursinus*, *Dorcopsis atrata*, *Dorcopsulus macleayi*, *Petrogale burbidgei* and *Pet. rothschildsi*) have apparently never been examined for cloacinine nematodes (Spratt & Beveridge, 2016), while for many other species only a few individuals have been examined. Griffith et al. (2000) estimated from species accumulation curves of nematodes in the pademelons *Thylogale stigmatica* and *Thyl. thetis*, that examination of five individuals was likely to reveal 87% of the parasites present. For a number of macropodoid species, only one or two individuals have been examined, again suggesting that the full extent of diversity within this nematode sub-family is currently under-estimated. As a number of the host species are either rare, threatened or occurring in relatively inaccessible geographical areas, obtaining parasite material from them in the future represents a challenge.

In recent years, the addition of allozyme and subsequently DNA sequence data for many species has both provided support for the identity of known species but has also revealed significant numbers of cryptic species, a process that is ongoing. Descriptive work currently lags behind molecular studies (Beveridge & Gasser, 2014). Recent molecular studies have also provided novel insights into phylogenetic relationships within the Cloacininae (Chilton et al., 2011, 2016a, b, c, 2017, 2018; Beveridge et al., 2020). These studies provide support for some existing taxonomic arrangements while at the same time presenting challenges for others (Beveridge et al., 2020). In particular, a molecular study of the tribe Labiostrongylinea by Chilton et al. (2011) provided no support for the separation of the genera *Labiosimplex*, *Labiostrongylus* and *Parazoniolaimus*, even though they are clearly distinguishable morphologically. Similarly, the morphologically uniform genus *Cyclostrongylus* appears to be paraphyletic (Beveridge et al., 2020). By contrast, molecular data provide support for the hypothesis that the morphologically diverse genus *Wallabinema* is para- or possibly polyphyletic (Beveridge et al., 2020). These inconsistencies remain to be resolved.

The current contribution attempts to provide an overview of the state of the systematics of the Cloacininae with keys to genera and species, synopses of each species including all relevant citations in the literature, the currently assessed host and geographical distribution and any associated DNA sequence data.

Taxonomic history of the Cloacininae

The definition of the Cloacininae used here is that of Lichtenfels (1980), which united, for the first time, all of the genera of nematodes found in the stomach and oesophagus of macropodid marsupials. In Lichtenfels' classification (1980), the Cloacininae fell within the family Chabertiidae (Popova, 1952) (in Skrjabin et al., 1952 as a sub-family), since it possessed two pairs of branches to the dorsal ray, in contrast to the Strongylidae Baird, 1853, which possessed three pairs of branches. Within the Chabertiidae, the Cloacininae was separated from the Chabertiinae in having cylindrical rather than globular buccal capsules, and from the Oesophagostominae Railliet, 1916 in having the externodorsal ray arising from the lateral trunk rather than from the dorsal ray and lacking a cervical collar (although this feature is not present in all genera of the Oesophagostominae). In Lichtenfels' classification (1980), all members of

the Chabertiidae possessed a J-shaped or Type-2 ovejector. There are however a few minor divergences from this pattern. Two species (among over 140) of the genus *Cloacina* von Linstow, 1898 have been found with the externo-dorsal ray arising from the dorsal ray (Beveridge, 2014) and a small number of species of *Cloacina* possess a Y-shaped or Type 1 ovejector (Beveridge, 1998a). A Y-shaped or Type 1 ovejector is also seen in some species of *Macropostrongylus* Yorke & Maplestone, 1926 and *Woodwardostrongylus* Wahid, 1964 (Beveridge, 1985, 1998b). Despite these exceptions, the Cloacininae appears to be differentiable from the related, marsupial–inhabiting Phascolostrongylinae Lichtenfels, 1980 in possessing filiform rather than conical deirids (Sukee et al., 2021), a character which also separates the Phascolostrongylinae from the Oesophagostominae, as well as lacking a dorsal gutter. Consequently, the definition provided by Lichtenfels (1980) appears to have held up moderately well in spite of the description of numerous new genera and species since 1980.

The earlier history of the classification of these nematodes is complex and has been summarised by Skrjabin et al. (1952, pp. 38–45). Yorke & Maplestone (1926) included all of the genera from macropodids known at that time (four genera) in the sub-family Trichoneminae Railliet, 1916, an arrangement accepted by Travassos & Vogelsang (1932). At the same time, the sub-family contained nematodes from equids, elephants, artiodactyls, tortoises and primates (Yorke & Maplestone, 1926). Erschov (1943) accepted the Trichonematidae Witenberg, 1925 (as Trichonemidae in the original publication) as a family, but placed the Australian genera of this family within a separate subfamily Quiloniinae Erschov, 1943 along with the nematodes of elephants and rhinoceroses. They were thus separated from the genera in equids which remained in the Trichonematidae.

The next major revision was that of Popova (1958) in which the family Cloacinidae Travassos, 1920 was employed with two sub-families, Cloacininae Stossich, 1899 and Zoniolaiminae Popova, 1952 (in Skrjabin et al., 1952, pp. 42–45, 138). The remaining genera from marsupials were placed in the family Trichonematidae, within the subfamily Murshidiinae Witenberg, 1925, containing Australian genera allocated to two tribes, Pharyngostrongylinea Popova, 1958 and Theilerianea Popova, 1958, again mixing genera from Australian and African hosts. Three genera (*Coronostrongylus* Johnston & Mawson, 1939; *Papillostrongylus* Johnston & Mawson, 1939; *Potorostrongylus* Johnston & Mawson, 1939) were not assigned to any subfamily by Popova (1958). In determining authorities for family subfamily names cited above, it appears that the Principle of Coordination of the ICZN (Article 36) had not been followed. Yamaguti (1961) elevated the Pharyngostrongylinea to familial status as the Pharyngostrongylidae, a change not accepted by subsequent authors.

Lichtenfels (1980), while incorporating most of the Australian genera in the now well-defined subfamily Cloacininae, utilised some of the available names in dividing the genera into four tribes: Cloacininea, Macropostrongylinea, Pharyngostrongylinea and Zoniolaiminea. Subsequently, the additional tribes Labiostrongylinea and Coronostrongylinea were erected by Beveridge (1983, 1986d).

The various tribes were erected almost exclusively on a phenetic basis, although the erection of the Coronostrongylinea was based on a morphological phylogenetic analysis (Beveridge, 1986d). However, more recent morphological and molecular phylogenetic analyses have provided little support for the current taxonomic arrangement (Beveridge et al., 2020). Relationships between genera within this sub-family clearly warrant additional investigation and consequently, the genera reviewed here are treated in alphabetical order, without being assigned to a particular tribe.

Molecular studies have provided compelling evidence (Chilton et al., 2018; Beveridge et al., 2020) that *Molinonema* Beveridge, 1986 , currently with two species, is paraphyletic and this conclusion is supported by morphological data (Beveridge et al., 2020). Consequently, a new genus, *Sacculostrongylus* n. gen., has been erected here for *M. ochetocephala* Beveridge, 1986. The same molecular studies also indicate that *Wallabinema* Beveridge, 1983 is polyphyletic, an unsurprising result given the morphological diversity within the genus (Beveridge, 1983). However, sequence data are not available for all species. In spite of this deficiency, five species found primarily in pademelons (*Thylogale* spp.) form a highly distinctive morphological group within the genus. Here, they are separated in a new genus, *Thylicostrongylus* n. gen. The position of *Wallabinema labiatum* (Johnston & Mawson, 1939) remains ambiguous and it has been retained for the time being within *Wallabinema*.

Methods

All relevant publications on cloacinine nematodes were reviewed as well as extensive collections of material held in the Australian Helminthological Collection (AHC) of the South Australian Museum, Adelaide (SAM). A list of all genera and their provisional allocation to tribes is provided in **Table 1**.

A definition of the sub-family and relatively detailed generic diagnoses are provided, but for species, only the key

characteristic features are listed. For small genera (2–3 species), the species synopses are quite brief, but for very large genera (*Cloacina*), more extensive synopses are required to differentiate species.

The illustrations provided are intended to show the principal morphological features of each genus only. It is not practicable to include illustrations of each species. However, the principal morphological features needed to identify species within each genus, following the keys, are shown in the illustrations. Most of the line drawings were copied from existing publications and were re-drawn in a uniform format. In some instances, original drawings were prepared from additional material.

As far as practicable, all citations of a particular species in the literature have been included. Citations are arranged in chronological order and in instances where multiple publications are cited by the same first author, these are listed on the basis of alphabetical names of authors. Taxonomic citations listed under each species do not include purely molecular studies unless they provide additional host or geographical information for a particular species. However, all such molecular studies are cited in the accompanying section of comments where appropriate. The checklist of Spratt & Beveridge (2016) has only been cited if it contains novel host data based on museum specimens.

Authorities for parasite names have been provided in the text but not in the captions to figures.

The distribution for each species is based on the state/territory/province from which collections are known. In instances where additional unpublished data are available, museum registration numbers are cited. Australian state and territory abbreviations and contractions used are as follows: ACT: Australian Capital Territory; NSW: New South Wales; NT: Northern Territory; Qld: Queensland; SA: South Australia; Tas: Tasmania; Vic: Victoria; WA: Western Australia. In the geographical distributions, "Vic" and "Tas" are treated as contractions for uniformity of style. Due to the size of Western Australia, regional divisional names, Kimberley and Pilbara, as well as informal terms (eg southwestern) have been used. In the case of the Northern Territory, the division between the tropical, humid north and the arid southern regions has been indicated by the colloquial terms Top End and Central Australia, both of which are in current use. For New Guinea, the eastern part is referred to as Papua New Guinea (PNG) and the western, Indonesian part as Western New Guinea.

The status of type specimens primarily follows usage in the original publication or, if absent, from labels in bottles or on slides and entries in the South Australian Museum database. Older descriptions may include "types" or "cotypes" and, although the latter term is not recognised in the International Code of Zoological Nomenclature (ICZN Recommendation 73E), these terms have been included here in inverted commas unless specific lecto- or para-lectotypes have subsequently been designated.

The institutions holding type material are listed in **Table 2**. Since some species were described, the name of the institution holding type material has sometimes changed. Type specimens formerly held by the Liverpool School of Tropical Medicine and the Commonwealth (International) Institute of Parasitology have been transferred to the British Museum (Natural History) (also known as The Natural History Museum, London) and only the current registration data are provided. The earlier acronym for the Natural History Museum (BMNH) has more recently been changed to NHMUK. However, all specimens referred to below have the acronym BMNH in the relevant publications. To avoid confusion, the acronym BMNH has been used here. Material formerly held at the School of Tropical Medicine and Hygiene of the University of Sydney has been transferred to the Queensland Museum, Brisbane and the relevant registration numbers in the Queensland Museum are cited herein. Following the transfer of the United States National Parasite Collection (USNPC) from the Department of Agriculture to the United States National Museum, all specimens have been assigned new registration numbers and these are available on-line. To avoid any confusion, the USNPC numbers published originally are included here.

At SAM, type specimens were initially listed in the Vermes series –"V" and other specimens were entered as part of the Australian Helminthological Collection (AHC) held in the same museum. Specimens in the Vermes series have subsequently been incorporated into the AHC by adding the prefix 4- to the V number. Specimens on slides, with the prefix "S", previously in a separate slide category, have been incorporated into the AHC with the prefix "2". To avoid confusion, the type data in relevant publications has been included here.

Host nomenclature follows Jackson & Groves (2015) for Australian mammals and Flannery (1995) for those found in New Guinea. In the case of the rock wallabies (*Petrogale* spp.), the taxonomic status of some species has not been resolved and consequently sub-specific names and names of "races" have been utilised (Jackson & Groves, 2015). A list of host genera and the abbreviations or contractions used in the text is provided in **Table 3** along with appreviations of nematode generic names. A list of host species with both scientific and common names is provided in **Table 4**. There have been many changes in host taxonomy so in instances where there is the possibility of confusion, the former name of the host is included in parentheses. Comments on host distributions are based on van

Dyck & Strahan (2008) for Australia and Flannery (1995) for New Guinea.

A comments section is provided only where additional information on identification, distribution or hosts is likely to be useful.

Two new genera have been erected and the new generic names registered in Zoobank. (Isid:zoobank.org:pub:FFC305DB-4178-442A-BD44-500AF-5668A9D)

Morphological terminology: Generic diversity within the Cloacininae is based primarily on features of the perioral region, buccal cavity and oesophagus. While the differential features of oesophageal morphology are relatively uncomplicated (see Beveridge et al., 2020), the homology of perioral structures, listed in a morphological phylogenetic analysis of the sub-family by Beveridge et al. (2020), has not been established and consequently the terminology used for these structures is not entirely consistent. The perioral structures currently used as generic criteria are the leaf crowns, collars, lips and teeth as well as some features of the buccal capsule (Beveridge et al., 2020).

Leaf crowns.

Although a leaf crown (or corona radiata) is a characteristic feature of many strongyloid nematodes (Chitwood, 1950; Skrjabin et al., 1952), there appear to be no precise definitions of what constitutes a leaf crown. Based on the features of the Strongylidae described by Skrjabin et al. (1952) and Lichtenfels (1980), an external leaf crown has petaloid elements arising from the anterior margin of the buccal capsule. External leaf crowns, usually composed of many elements, are found in a number of cloacinine genera (*Arundelia*, *Beveridgea* (Fig. 1 G), *Foliostoma* (Fig. 20 J), *Tethystrongylus* (Fig. 38 C) and encircle the anterior extremity of the buccal capsule. In one species, *Papillostrongylus barbatus* (Fig. 29 M), the leaf crown elements are arranged in two lateral arcs. Beveridge (1982) noted that in the case of the "external leaf crown" elements of *Pharyngostrongylus*, the external surface of each element arose not from the extremity of the buccal capsule but from the surrounding labial region (Figs 32 M–R). The term "labial crown" was suggested and applied also to the genera *Mbaisonema* (Fig. 29 B), *Parapharyngostrongylus* (Fig. 31 I), *Thylostrongylus* (Fig. 39 B) and here also to *Trigonostonema* (Figs 39, M, K). Internal leaf crowns, which, in the Cloacininae, arise from the internal wall of the buccal capsule, are present in the genera *Cloacina* (Figs 4 A. I) and *Cervonemella* (Fig. 2 G).

Collars

In many genera, the peri-oral region is separated from the remainder of the nematode body by a distinct suture and has been termed a "cephalic collar". In *Rugopharynx*, there is an additional collar, internal to the cephalic collar (Figs. 36 B, E), which is continuous but may in some species be partially subdivided. This structure has been termed a "labial collar" (Beveridge, 1982) and is present also in *Popovastrongylus* (Figs 33 B, C). In two genera, *Pararugopharynx* (Figs 30 G, H) and *Spirostrongylus* (Fig. 37 L), the labial collar is considered to be lobed (Beveridge, 1982). In other genera, such as *Zoniolaimus*, no collars may be present (Figs 39 B, C). In *Paralabiostrongylus*, there are two collars, well posterior to the cephalic collar (Fig. 31 C). They are referred to here as "cervical collars". *Parazoniolaimus* possesses a cervical collar which is disc-like and extends beyond the nematode body (Fig. 31 L).

Lips

The term "lip" has been applied to a number of different types of peri-oral structures. The family Cloacinidae was defined by Chabaud (1965) as possessing six "lips", but in the type genus, the lips are inflations of the cuticle joining the tip of the internal leaf crown to the peri-oral region (Beveridge, 1998a) (Fig. 13 A). A more detailed discussion of "lips" in the Cloacininae was provided by Beveridge (1983). He distinguished genera possessing elongated lips, circular to ovate in cross section, with a prominent pulp cavity, such as those seen in *Labiostrongylus* and related genera (Fig. 26 B) from flap-like lips in which a pulp cavity is generally absent, such as those present in *Zoniolaimus* and related genera (Fig. 39 C) and used this character to separate a new tribe, Labiostrongylinea from the existing Zoniolaiminea (Beveridge, 1983). Subsequent molecular analyses have suggested that lips with prominent pulp cavities are homoplasious (Beveridge et al., 2020). However, it was noted that the "lips" of the type seen in species of *Zoniolaimus* were rather similar to the labial crown elements of *Pharyngostrongylus* (Beveridge, 1983). For these reasons, additional clarification of the homology of these labial structures is needed.

Teeth

Oesophageal teeth projecting into the base of the buccal capsule are present in a number of Strongyloid genera (Lichtenfels, 1980) and similar structures exist within the Cloacininae, particularly in the genus *Cloacina* (Figs 5Q, 11F). Additional structures, also referred to as teeth, may arise near the anterior extremity of the buccal capsule and project into the mouth opening, as in *Parapharyngostrongylus* (Fig. 31 J) and *Thallostonema* (Figs 38 I, J), or may act as supports for submedian lips in *Zoniolaimus* (Figs 39B, D). Mawson (1961b) referred to "teeth" in the mid-oesophageal region of certain species of *Cloacina*, but Beveridge (1998a) preferred the term "denticles" for these structures (Figs 8 G, P).

Systematics

Strongyloidea Weinland

Chabertiidae (Popova)

Cloacininae Stossich

Nematodes of variable size; four sub-median papillae and two amphids present; labial papillae absent; buccal capsule cylindrical, either heavily sclerotized or, if poorly sclerotized, supported by prominent radial musculature; many genera with either internal or external leaf crowns; dorsal gutter lacking; deirids setiform; oesophagus claviform or with terminal bulb or terminal cylindrical region; bursa with ventro-ventral and ventro-lateral rays apposed; externo-lateral ray divergent, usually shorter than remaining lateral rays; medio-lateral and postero-lateral rays apposed; externo-dorsal ray arising from lateral trunk (in two species of *Cloacina*, arising from dorsal trunk); dorsal ray with two pairs of branches; vulva immediately anterior to anus; ovejector J-shaped (Type 2) or rarely Y-shaped (Type 1); uteri pro-delphic; egg thin shelled, ellipsoidal.

Table 1. Alphabetical list of genera of the Cloacininae and provisional allocation to tribes

Alocostoma Mawson, 1979	Macropostrongylinea
Arundelia Mawson, 1977	Cloacininea
Beveridgea Mawson, 1980	Cloacininea
Cassunema Beveridge & Johnson, 1981	Zoniolaiminea
Cervonemella Beveridge, 2001	Cloacininea
Cloacina von Linstow, 1898	Cloacininea
Corollonema Beveridge & Chilton, 1998	Coronostrongylinea
Coronostrongylus Johnston & Mawson, 1939	Coronostrongylinea
Cyclostrongylus Johnston & Mawson, 1939	Pharyngostrongylinea
Dorcopsinema Mawson, 1977	Labiostrongylinea
Dorcopsistrongylus Smales, 1982	Pharyngostrongylinea
Foliostoma Beveridge & Johnson, 1981	Macropostrongylinea
Labiomultiplex Smales, 1994	Labiostrongylinea
Labiosimplex Smales, 1994	Labiostrongylinea
Labiostrongylus Yorke & Maplestone, 1926	Labiostrongylinea
Macroponema Mawson, 1978	Macropostrongylinea
Macropostrongylus Yorke & Maplestone, 1926	Macropostrongylinea
Mbaisonema Beveridge, 1997	Coronostrongylinea
Monilonema Beveridge & Johnson, 1981	Macropostrongylinea
Papillostrongylus Johnston & Mawson, 1939	Coronostrongylinea
Paralabiostrongylus Smales, 1982	Labiostrongylinea
Parapharyngostrongylus Beveridge, 1982	Pharyngostrongylinea
Pararugopharynx Magzoub, 1964	Pharyngostrongylinea
Parazoniolaimus Johnston & Mawson, 1939	Labiostrongylinea
Pharyngostrongylus Yorke & Maplestone, 1926	Pharyngostrongylinea
Popovastrongylus Mawson, 1997	Coronostrongylinea
Potorostrongylus Johnston & Mawson, 1939	Labiostrongylinea
Rugopharynx Mönnig, 1927 (=*Rugonema* Beveridge, 1989)	Pharyngostrongylinea
Rugostrongylus Beveridge, 1982	Pharyngostrongylinea
Sacculostrongylus n. gen.	Macropostrongylinea
Spirostrongylus Yorke & Maplestone, 1926	Pharyngostrongylinea
Tethystrongylus Beveridge, 1983	Zoniolaiminea
Thallostonema Beveridge, 1983	Zoniolaiminea
Thylicostrongylus n. gen.	Zoniolaiminea
Thylonema Beveridge, 1981	Coronostrongylinea
Thylostrongylus Beveridge, 1982	Pharyngostrongylinea
Trigonostonema Beveridge, 1981	Macropostrongylinea
Wallabinema Beveridge, 1983	Zoniolaiminea
Woodwardostrongylus Wahid, 1964	Pharyngostrongylinea
Zoniolaimus Cobb, 1898	Zoniolaiminea

***Genus inquirendum**: Maplestonema* Johnston & Mawson, 1939

Table 2. List of institutions currently holding type material

AM – Australian Museum, Sydney.
ANWC – Australian National Wildlife Collection, CSIRO, Canberra.
BBM – Bernice Bishop Museum, Honolulu.
BMNH – British Museum (Natural History), London.
MNHNP – Muséum national d'Histoire naturelle, Paris.
MNKB – Museum für Naturkunde, Berlin.
MZB – Bogor Zoological Museum, Bogor, Indonesia.
OVRI – Onderstepoort Veterinary Research Institute, Pretoria, South Africa.
QM – Queensland Museum, Brisbane.
SAM - South Australian Museum, Adelaide.
USNPC (USMHC, USNM) – United States National Parasite Collection (now the United States National Museum).
WAM – Western Australian Museum, Perth.
ZIMG - Zoological Museum, University of Greifswold, Germany.

Table 3. Abbreviations and contractions of nematode and host generic names used in the text

Nematode genera:

Alocostoma Mawson, 1979. . . . . .*A.*
Arundelia Mawson, 1977 . . . . . *Ar.*
Beveridgea Mawson, 1980 . . . . . .*B.*
Cassunema Beveridge & Johnson, 1981 . . . . . *Ca.*
Cervonemella Beveridge, 2001 . . . . . *Ce.*
Cloacina von Linstow, 1898 . . . . . .*C.*
Corollonema Beveridge & Chilton, 1998 . . . . . *Corol.*
Coronostrongylus Johnston & Mawson, 1939 . . . . . *Co.*
Cyclostrongylus Johnston & Mawson, 1939 . . . . . *Cy.*
Dorcopsinema Mawson, 1977 . . . . . *D.*
Dorcopsistrongylus Smales, 1982 . . . . . *Do.*
Foliostoma Beveridge & Johnson, 1981 . . . . . .*F.*
Labiomultiplex Smales, 1994. . . . . .*Lm.*
Labiosimplex Smales, 1994. . . . . *Ls.*
Labiostrongylus Yorke & Maplestone, 1926 . . . . . .*L.*
Macroponema Mawson, 1978 . . . . . *M.*
Macropostrongylus Yorke & Maplestone, 1926 . . . . .*Ma.*
Mbaisonema Beveridge, 1997 . . . . . .*Mb.*
Monilonema Beveridge & Johnson, 1981. . . . . .*Mo.*
Papillostrongylus Johnston & Mawson, 1939 . . . . . .*P.*
Paralabiostrongylus Smales, 1982 . . . . . *Pl.*
Parapharyngostrongylus Beveridge, 1982. . . . . .*Par.*
Pararugopharynx Magzoub, 1964 . . . . . *Pr.*
Parazoniolaimus Johnston & Mawson, 1939 . . . . . *Pz.*
Pharyngostrongylus Yorke & Maplestone, 1926 . . . . .*Ph.*
Popovastrongylus Mawson, 1997 . . . . . .*Pop.*
Potorostrongylus Johnston & Mawson, 1939 . . . . . .*Pot.*
Rugopharynx Mönnig, 1927 (=*Rugonema* Beveridge, 1989)*R.*
Rugostrongylus Beveridge, 1982 . . . . . *Ru.*
Sacculostrongylus n. gen. . . . . *Sa.*
Spirostrongylus Yorke & Maplestone, 1926 . . . . . *Sp.*
Tethystrongylus Beveridge, 1983 . . . . . .*T.*
Thallostonema Beveridge, 1983. . . . . *Th.*
Thylicostrongylus n. gen.. . . . . *Ty.*
Thylonema Beveridge, 1981 . . . . . *Tl.*
Thylostrongylus Beveridge, 1982 . . . . . *Ts.*
Trigonostonema Beveridge, 1981 . . . . . *Tr.*
Wallabinema Beveridge, 1983 . . . . . *W.*
Woodwardostrongylus Wahid, 1964 . . . . . .*Wo.*
Zoniolaimus Cobb, 1898. . . . . .*Z.*

Host genera

Aepyprymnus Garrod 1875. . . . . .*Aep.*
Dendrolagus Müller, 1840 . . . . . .*Dend.*
Dorcopsis Schlegel & Müller, 1845 . . . . . *Dc.*
Dorcopsulus Matschie, 1916 . . . . . *Dp.*
Lagorchestes Gould, 1841 . . . . . *La.*
Lagostrophus Thomas, 1887 . . . . . *Lago.*
Macropus Shaw, 1790 . . . . . *Mac.*
Notamacropus Dawson & Flannery, 1985. . . . . *N.*
Onychogalea Gray, 1841. . . . . *On.*
Osphranter Gould, 1842 . . . . . *O.*
Petrogale Gray, 1837 . . . . . *Pet.*
Potorous Desmarest, 1804 . . . . . *Pot.*
Setonix Lesson, 1842 . . . . . *Set.*
Thylogale Gray, 1837 . . . . . *Thyl.*
Wallabia Trouessart, 1905 . . . . . .*Wal.*

Table 4. Hosts of cloacinine nematodes (scientific and common names)

Family POTOROIDAE Gray, 1821	
Tribe Bettongiini Flannery & Archer, 1987	
Aepyprymnus rufescens (Gray, 1837)	rufous bettong
Bettongia gaimardi (Desmarest, 1822)	eastern bettong
Bettongia penicillata Gray, 1837	brush-tailed bettong
Bettongia tropica Wakefield, 1967	northern bettong
Tribe Potoroini Gray, 1821	
Potorous tridactylus (Kerr, 1792)	long-nosed potoroo
Family MACROPODIDAE Gray, 1821	
Subfamily Macropodinae Gray, 1821	
Tribe Dendrolagini Flannery, 1989	
Dendrolagus bennettianus DeVis, 1887	Bennett's tree kangaroo
Dendrolagus dorianus Ramsay, 1883	Doria's tree kangaroo
Dendrolagus goodfellowi Thomas, 1908	Goodfellow's tree kangaroo
Dendrolagus inustus Müller, 1840	grizzled tree kangaroo
Dendrolagus lumholtzi Collett, 1883	Lumholtz's tree kangaroo
Dendrolagus matschiei Forster & Rothschild, 1907	Huon tree kangaroo
Dendrolagus mbaiso Flannery, Boeadi & Szalay, 1995	dingiso
Dendrolagus scottae Flannery & Seri, 1990	tenkile
Petrogale assimilis Ramsay, 1877	allied rock wallaby
Petrogale brachyotis (Gould, 1841)	western short-eared rock wallaby
Petrogale coenensis Eldridge & Close, 1992	Cape York rock wallaby
Petrogale concinna Gould, 1842	Nabarlek rock wallaby
Petrogale godmani Thomas, 1923	Godman's rock wallaby
Petrogale herberti Thomas, 1926	Herbert's rock wallaby
Petrogale inornata Gould, 1842	unadorned rock wallaby
Petrogale lateralis Gould, 1840	black-footed rock wallaby
Petrogale lateralis pearsoni Thomas, 1922	Pearson Island rock wallaby
Petrogale mareeba Eldridge & Close, 1992	Mareeba rock wallaby
Petrogale penicillata (Gray, 1827)	brush-tailed rock wallaby
Petrogale persephone Maynes, 1982	Proserpine rock wallaby
Petrogale purpureicollis Le Souef, 1924	purple-necked rock wallaby
Petrogale sharmani Eldridge & Close, 1992	Mount Claro rock wallaby
Petrogale wilkinsi Thomas, 1926	eastern short-eared rock wallaby
Petrogale xanthopus (Gray, 1855)	yellow-footed rock wallaby
Thylogale billardierii (Desmarest, 1822)	rufous-bellied pademelon
Thylogale browni (Ramsay, 1877)	New Guinea pademelon
Thylogale brunii (Schreber, 1778)	dusky pademelon
Thylogale calabyi Flannery, 1992	Calaby's pademelon
Thylogale stigmatica (Gould, 1860)	red-legged pademelon
Thylogale thetis (Lesson, 1827)	red-necked pademelon

Table 4. Hosts of cloacinine nematodes (scientific and common names) (continued)

Tribe Dorcopsini Prideaux &Warburton, 2010	
Dorcopsis hageni Heller, 1897	white-striped dorcopsis
Dorcopsis luctuosa D'Albertis, 1874	grey dorcopsis
Dorcopsis muelleri (Schlegel, 1866)	brown dorcopsis
Dorcopsulus vanheurni (Thomas, 1922)	small dorcopsis
Tribe Macropodini Gray, 1821	
Lagorchestes conspicillatus Gould, 1842	spectacled hare wallaby
Lagorchestes hirsutus Gould, 1844	rufous hare wallaby
Macropus fuliginosus (Desmarest, 1817)	western grey kangaroo
Macropus giganteus Shaw, 1790	eastern grey kangaroo
Notamacropus agilis (Gould, 1842)	agile wallaby
Notamacropus dorsalis (Gray, 1837)	black-striped wallaby
Notamacropus eugenii (Desmarest, 1817)	tammar wallaby
Notamacropus irma (Jourdan, 1837)	western brush wallaby
Notamacropus parma (Waterhouse, 1846)	parma wallaby
Notamacropus parryi (Bennett, 1835)	whip-tailed wallaby
Notamacropus rufogriseus (Desmarest, 1817)	red-necked wallaby
Onychogalea fraenata (Gould, 1840)	bridled nail-tail wallaby
Onychogalea unguifera (Gould, 1840)	northern nail-tail wallaby
Osphranter antilopinus (Gould, 1842)	antilopine wallaroo
Osphranter bernardus (Rothschild, 1904)	black wallaroo
Osphranter robustus (Gould, 1840)	common wallaroo
Osphranter robustus woodwardi (Thomas, 1901)	northern wallaroo
Osphranter rufus (Desmarest, 1822)	red kangaroo
Wallabia bicolor (Desmarest, 1804)	swamp wallaby
Tribe Setonichini Jackson & Groves, 2015	
Setonix brachyurus (Quoy & Gaimard, 1830)	quokka
Subfamily Lagostrophinae Flannery, 1989	
Tribe Lagostrophini Flannery, 1989	
Lagostrophus fasciatus (Péron & Lesueur, 1807)	banded hare wallaby

Key to genera of the Cloacininae

1a. Cephalic papillae bipartite (Cloacininea) (Figs 1G, 1I, 2H, 3C, 3H) 2
1b. Cephalic papillae not bipartite 5

2a. Anterior intestine projects to envelop oesophageal bulb (Fig. 2E) . . . *Cervonemella*
2b. Anterior intestine does not project to envelop oesophageal bulb 3

3a. Buccal capsule deeper than wide, anterior margin notched (Fig. 1G) . . . . . .*Beveridgea*
3b. Buccal capsule not deeper than wide, anterior margin not notched. 4

4a. Cuticular annulations prominent, V-shaped posteriorly (Fig. 1I) . . . . . *Arundelia*
4b. Cuticular annulations, if prominent, lobed (Figs 3K, 4R) . . . . . .*Cloacina*

5a. Cephalic papillae prominently truncated (Figs 1B, 1C) . . . . . *Alocostoma*
5b. Cephalic papillae not prominently truncated. . . .6

6a. Oesophagus with bulb cylindrical, elongate and with intestinal cells extending anteriorly to enclose bulb (Figs 31G, 32A, 37A) 7
6b. Oesophagus with non-cylindrical, elongate bulb .9

7a. Prominent dorsal and ventral teeth at anterior margin of buccal capsule (Figs 31H, I) . . . . . *Parapharyngostrongylus*
7b. Without prominent dorsal and ventral teeth at anterior margin of buccal capsule 8

8a. Prominent labial crown present (Figs 32M-R). . . . . *Pharyngostrongylus*
8b. Prominent labial crown absent (Figs 37B, C) . . . . . *Rugostrongylus*

9a. Oesophagus broad and clavate anterior to nerve ring; slender and sinuous posterior to nerve ring (Fig. 38F) . . . . . *Thallostonema*
9b. Oesophagus not of this type 10

10a.Oesophageal bulb lined with either 3 individual or 3 pairs of sclerotized plates (Figs 18A, 30E, 34A, 37J, 39N, 40A, 41D, 43A). 11
10b. Oesophageal bulb without sclerotised plates . 20

11a. Oesophagus with additional fusiform bulb in mid-region (Fig. 41A) . . . *Zoniolaimus*
11b. Oesophagus without additional fusiform bulb in mid-region 12

12a. Buccal capsule with transverse striations (Figs 18B-D, 30F, G, 38B) 13
12b. Buccal capsule without transverse striations . 15

13a. Leaf crown of numerous tiny elements; nerve ring in anterior oesophageal region . . . . . .*Tethystrongylus*
13b. Labial crown of 8 elements (Figs 40A, C) . . . . . .*Thylostrongylus*
13c. Leaf crown or labial crown absent. 14

14a. Labial collar divided into 10 lobes; body not coiled; alae absent (Figs 30 F-H) . . . . . *Pararugopharynx*
14b. Labial collar absent; body usually coiled or with lateral alae (Figs 18A, F-H) . .*Cyclostrongylus*

15a. Labial collar divided into 10 lobes (Figs K, L); body coiled; ventral ala present (Fig. 37M) . . . . . *Spirostrongylus*
15b. Labial collar absent; body not coiled 16

16a. Lips prominent with pulp cavity; papillae borne on lips (Figs 34B-D) . . . *Potorostrongylus*
16b. Lips absent, or, if present, flap-like; papillae not borne on lips 17

17a. Internal leaf crown present consisting of numerous elements (Fig. 2B) . . . . *Cassunema*
17b. Internal leaf crown absent 18

18a. Nerve ring anterior to oesophageal isthmus (Figs 41A, D, J) . . . . . .*Wallabinema*
18b. Nerve ring surrounds oesophageal isthmus . 19

19a. Labial crown present (Figs 40E, F) . . . . . .*Thylostrongylus*
19b. Labial crown absent (Figs 39, K-O) . . . . . *Thylicostrongylus* n. gen.

20a. Lips present with prominent pulp cavity (Figs 19B-D, 22A-C, 24D) 21
20b. Lips absent 26

21a. Two prominent cervical collars present (Fig. 31C) . . . . . *Paralabiostrongylus*
21b. Single, fleshy labial collar or labial collar absent. 22

22a. Disc-like expansion of cuticle present posterior to lips (Fig. 31L) . . . *Parazoniolaimus*
22b. Disc-like expansion absent 23

23a. Single fleshy labial collar present (Fig. 19A); lips arise internal to collar (Figs 19D, G). . . . . *Dorcopsinema*
23b. Labial collar absent (Figs 22A–C) 24

24a. Nerve ring near base of oesophagus with small bulb posterior to nerve ring (Figs 22D–G) . . . . . *Labiomultiplex*
24b. Nerve ring in anterior oesophageal region . . 25

25a. Interlabia present (Fig. 26D) . . . *Labiostrongylus*
25b. Interlabia absent (Fig. 23C) . . . . *Labiosimplex*

26a. Mouth opening with dorso-ventral rows of paired denticles (Figs 42D, G, H) . . . . . *Woodwardostrongylus*
26b. Mouth opening without rows of denticles . . 27

27a. Mouth opening with paired, triangular lateral projections (Figs 30A, B) . . . *Papillostrongylus*
27b. Mouth opening without paired, triangular lateral projections 28

28a. Two or more blind, tubular structures extending from buccal capsule to mid-oesophageal region (Figs 29E, 37G) . . . 29
28b. Tubular structures lacking 30

29a. Two tubular structures (Fig. 29E); leaf crown present (Fig. 29F) . . . . . *Monilonema*
29b. Eight tubular structures (Figs 37G, I): leaf crown absent (Figs 37F, H) . . . . . *Sacculostrongylus* n. gen.

30a. External leaf crown present 31
30b. External leaf crown absent. 34

31a. Prominent sclerotized ring at base of buccal capsule (Figs 17E, 20K) 32
31b. No prominent sclerotized ring at base of buccal capsule 33

32a. Leaf crown of 8 elements (Fig. 17F); oesophageal bulb ovoid (Fig. 17E) . . . . . *Corollonema*
32b. Leaf crown of numerous, fine elements (Figs 20J, K); oesophageal bulb cylindrical (Fig. 20H) . . . . . .*Foliostoma*

33a. Oesophageal bulb ovoid (Fig. 29A); anterior intestinal cells not enlarged (Fig. 29A) . . . . . *Mbaisonema*
33b. Oesophageal bulb sub-cyclidrical (Fig. 40 I); anterior intestinal cells enlarged, enclosing bulb (Fig. 40 I) . . . . . *Trigonostonema*

34a. Buccal capsule heavily sclerotized either fully or in lower half. 35
34b. Buccal capsule poorly sclerotized, usually with strong external muscular supports . . . 37

35a. Lower half of buccal capsule sclerotized (Fig. 17B) . . . . . *Coronostrongylus*
35b. Entire buccal capsule wall sclerotized 36

36a. Anterior intestine enlarged to surround oesophageal bulb (Fig. 20E) . *Dorcopsistrongylus*
36b. Anterior intestine not enlarged. . . .*Rugopharynx*

37a. Oesophageal lining with prominent longitudinal or transverse folds, or small globular ornamentation (Figs 27A–J) . . . *Macroponema*
37b. Oesophageal lining without prominent ornamentation. 38

38a. Oesophageal bulb ovoid (Figs 33A, D, H) . . . . . *Popovastrongylus*
38b. Oesophageal bulb elongate or clavate (Figs 28A–F, 39A), ... 39

39a. Nerve ring in anterior oesophageal region (Figs 28A–F); cephalic papillae conical (Figs 28G–I) . . . . . *Macropostrongylus*
39b. Nerve ring encircles oesophageal isthmus (Fig. 39A); cephalic papillae bilobed in apical views (Figs 39D, E, H) . . . .*Thylonema*

Species descriptions

Alocostoma Mawson, 1979

Type species: A. *clelandi* (Johnston & Mawson, 1939).
Other species: *A. propinquum* Beveridge, 1986.
Generic diagnosis: cephalic collar present; cephalic papillae cylindrical, truncate, lacking setae (Figs 1 B, C); mouth opening circular to sub–triangular; labial collar finely striated internally; buccal capsule longer than wide, poorly sclerotized, lacking transverse striations, without annulus, supported externally by prominent bands of radial muscles (Fig.1 B); oesophageal corpus elongate; isthmus indistinct, bulb fusiform; nerve ring in anterior oesophageal region; deirid post-buccal; excretory pore posterior to nerve ring; anterior intestine enlarged but not enclosing oesophageal bulb (Fig. 1A); bursa without sclerotized bosses; gubernaculum absent; spicules elongate, alate; ovejector J-shaped.
Comments: *Alocostoma* is a small but highly distinctive genus, immediately recognisable by the truncated cephalic papillae. The males of the two species are distinguishable from the shape of the dorsal ray of the bursa, but the females are very similar and can only be distinguished by measurements.

Key to species of *Alocostoma*

1a. Dorsal lobe of bursa shorter than lateral lobes; dorsal ray short (Fig. 1 E); vagina 0.55–0.68 mm . . . . . *A. clelandi*
1b. Dorsal lobe of bursa longer than lateral lobes; dorsal ray elongate (Fig. 1 D); vagina 0.85–1.06 mm . . . . . *A. propinquum*

Alocostoma clelandi (Johnston & Mawson, 1939)

Cyclostrongylus clelandi Johnston & Mawson, 1939b, pp. 518–519, figs 14–15; Skrjabin et al., 1952, p. 176; Popova, 1960, pp. 77–78, fig. 47; Yamaguti, p. 408; Mawson, 1977a, p. 19; Beveridge & Arundel, 1979, p. 72.
Alocostoma clelandi: Mawson, 1979, pp. 123–125, figs 1–11; Beveridge, 1986c, pp. 508–510, fig. 2; Arundel et al., 1990, p. 42; Beveridge et al., 1998, p. 483; Aussavy et al., 2011, p. 14; Schultz et al., 2011, p. 238; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240.
Type data: holotype and allotype SAM V1696.
Type locality: Coonamble, NSW (30° 57′S 148° 24′E).
Type host: *Macropus giganteus* Shaw, 1790.
Other hosts: *Osphranter robustus* (Gould, 1840); *Petrogale penicillata* (Gray, 1827).
Site in host: stomach.
Distribution: Qld, NSW, Vic.
Representative DNA sequence data: ITS1, 2: MG 865615–6.
Diagnostic features (Figs 1 E, 44 A): Males 7.8–14.5 mm; females 8.8–19.0 mm; dorsal lobe of bursa short; dorsal ray bifurcates at mid-length; lateral branchlets arise immediately after principal bifurcation; spicules 1.67–1.90 mm; vagina 0.55–0.68 mm; ovejector J-shaped.
Comments: This species is a common parasite of *Mac. giganteus* and is found less frequently in *O. robustus* (Beveridge et al., 1998). The single record from *Pet. penicillata* was from a captive animal released into an area of sympatry with *Mac. giganteus* (Schultz et al., 2011).

Alocostoma propinquum Beveridge, 1986

Alocostoma propinquum Beveridge, 1986c, pp. 506–508, fig. 1 (as *propinqua*); Beveridge et al., 1998, p. 483; Beveridge, 2020c, p. 5.
Type data: holotype SAM V3560, allotype SAM V3561, paratypes SAM AHC 13386, MNHNP 20HC.
Type locality: Pallamana Station via Charters Towers, Qld (20° 31′S 146° 32′E).
Type host: *Macropus giganteus* Shaw1790.
Other hosts: *Osphranter robustus* (Gould, 1840).
Site in host: stomach.
Distribution: Qld.
Representative DNA sequence data: ITS1, 2: MG 865617–8.
Diagnostic features (Figs 1 A–D): Males 7.9–12.3 mm; females 9.6–14.2 mm; dorsal lobe of bursa elongate; dorsal ray bifurcates at 1/3rd length; external branchlets arise from posterior half of internal branchlets; spicules 1.84–2.39 mm; vagina 0.85–1.06 mm; ovejector J-shaped.

Arundelia Mawson, 1977

Type species: *Ar. dissimilis* (Johnston & Mawson, 1939).
Generic diagnosis: Body with prominent transverse annulations, terminating posteriorly in V-shaped projections (Fig. 1 I); cephalic collar present; cephalic papillae very small, bipartite; mouth opening circular; external leaf crown of 6 elements; buccal capsule wider than long; walls heavily sclerotized, without transverse striations; dorsal lobe of oesophagus projects prominently into lumen of buccal capsule; oesophagus claviform; nerve ring and deirid in

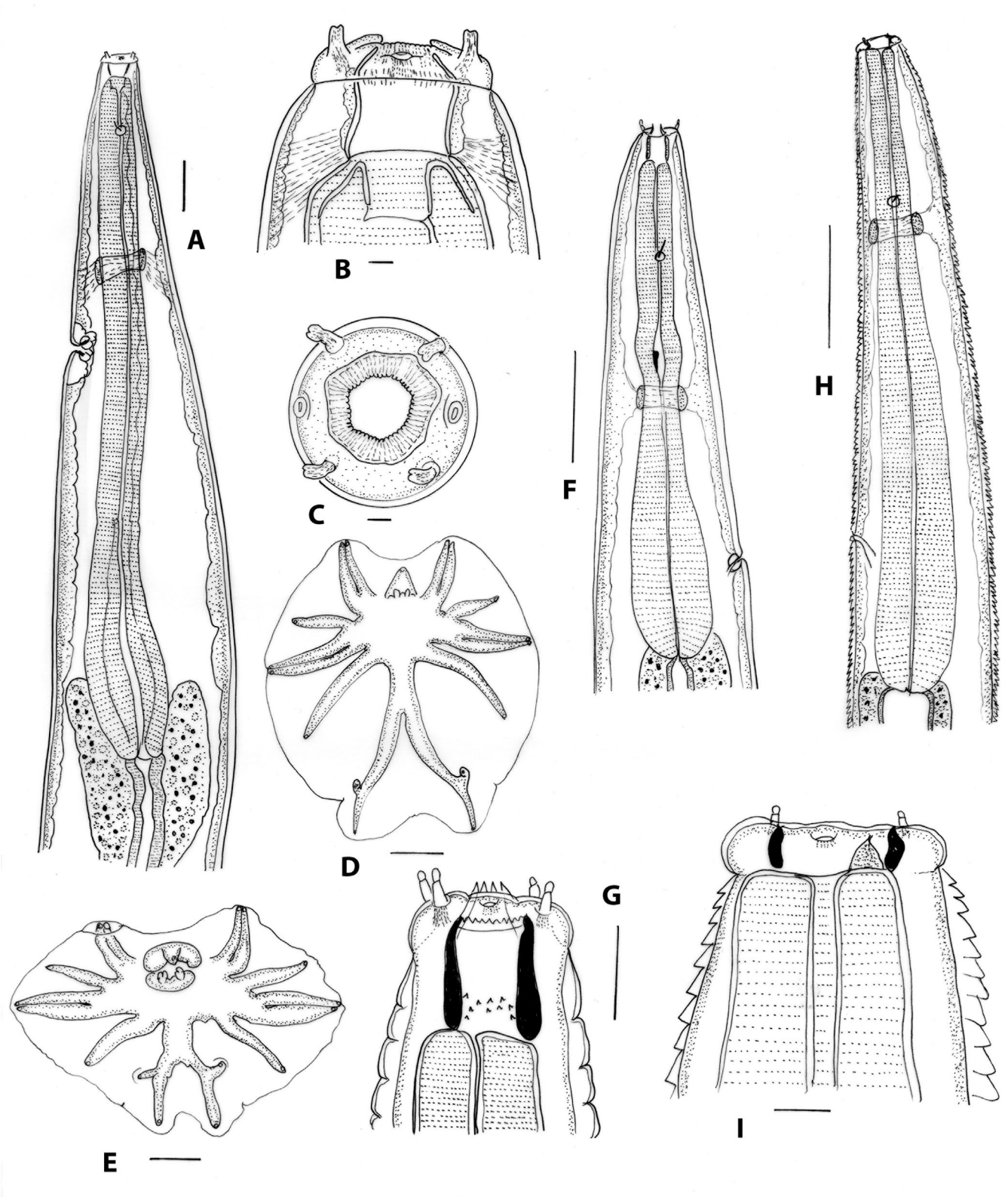


Fig. 1. Genera *Alocostoma*, *Arundelia* and *Beveridgea*. A, *Alocostoma propinquum*, anterior end, lateral view; B, *A. propinquum*, buccal capsule, lateral view; C, *A. propinquum*, anterior end, apical view; D. *A. propinquum*, bursa; E, *A. clelandi*, bursa; F, *Beveridgea corneri*, anterior end, lateral view showing oesophageal denticle; G, *B. corneri*, buccal capsule, lateral view; H, *Arundelia dissimilis*, anterior end, lateral view; I, *A. dissimilis*, buccal capsule, lateral view. (A–E from Beveridge, 1986d; F–G from Mawson, 1980; H, I. original).

Scale-bars: A, D–F, H, 0.1 mm; B, C, I, 0.01 mm; G, 0.03 mm.

anterior oesophageal region; excretory pore in posterior oesophageal region (Fig. 1H); bursa without sclerotized bosses; spicules elongate, alate; ovejector J-shaped.

Comments: This monotypic genus is readily distinguished by the prominently projecting annulations of the body. The oral features need additional study using scanning electron microscopy.

***Arundelia dissimilis* (Johnston & Mawson, 1939)**

Macropostrongylus dissimilis Johnston & Mawson, 1939b, p. 526.

Gelanostrongylus dissimilis: Popova, 1960, pp. 83–84, fig. 52.

Arundelia dissimilis: Mawson, 1977b, pp. 58–60, figs 41–44, 52; Beveridge et al., 1985, p. 378; Beveridge, 2016, p. 212; Spratt et al., 2017, p. 246.

Type data: "types" SAM AHC 41563.

Type locality: Lower Hawkesbury, NSW (33° 30′S 151° 10′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: Qld, NSW, Vic.

Representative DNA sequence data: ITS1, 2: MF284673.

Diagnostic features (Figs 1 H, I): Males 4.9–7.1 mm; females 6.9–8.3 mm; oesophagus 0.54–0.75 (male), 0.75–0.88 (female) mm; nerve ring 0.21–0.26 (m), 0.23–0.30 (f), excretory pore 0.40–0.46 (m), 0.36–0.58 (f), deirid 0.09–0.18 (m), 0.15–0.20 (f) mm from anterior end; spicules 0.70–0.75 mm; female tail 0.19–0.26 mm; vulva to posterior end 0.30–0.40 mm; egg ellipsoidal 0.130–0.132 x 0.065–0.070 mm.

Comments: Measurements provided were made by P.M. Mawson in her redescription of the species but were never published.

Beveridgea Mawson, 1980

Type species: *B. corneri* Mawson, 1980.

Generic diagnosis: cephalic collar present; cephalic papillae bipartite; mouth opening circular; external leaf crown of 8 elements; buccal capsule longer than wide; walls heavily sclerotized, without transverse striations; anterior margin notched; tiny denticles in posterior part of buccal capsule (Fig. 1 G); oesophagus claviform, with pre-neural swelling containing single denticle; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid anterior to nerve ring (Fig. 1 F); bursa without sclerotized bosses; spicules elongate, alate; gubernaculum present; ovejector J-shaped.

***Beveridgea corneri* Mawson, 1980**

Beveridgea corneri Mawson, 1980, pp. 81–82, figs 1–7; Speare et al., 1983, p. 90; Beveridge et al., 1998, p. 484.

Type data: holotype, allotype, SAM V1910.

Type locality: Elizabeth Downs Station, NT (13° 38′S 130° 29′E).

Type host: *Notamacropus agilis* (Gould, 1842).

Site in host: stomach.

Distribution: NT, Qld.

Diagnostic features (Figs 1 F, G): Males 4.7–5.7 mm; females 4.9–5.3 mm; ovejector J-shaped.

Comments: Mawson (1980) gave the type locality as Queensland rather than the Northern Territory.

Cassunema Beveridge & Johnson, 1981

Type species: *Cassunema exiguum* Beveridge & Johnson, 1981.

Generic diagnosis: cephalic collar present; submedian cephalic papillae domed, each with single short seta (Fig. 2 C); mouth opening dorsoventrally elongate; leaf crowns and teeth absent; buccal capsule as long as wide, poorly sclerotized, with series of internal longitudinal ridges at anterior extremity (Fig. 2 B); oesophageal corpus elongate; oesophageal bulb ovoid with 3 pairs of sclerotized plates; nerve ring, excretory pore and deirid in anterior oesophageal region; anterior region of intestine enlarged but not extending anteriorly to surround oesophageal bulb (Fig. 2 A); bursa without sclerotised bosses; spicules elongate, alate; ovejector J-shaped.

***Cassunema exiguum* Beveridge & Johnson, 1981**

Cassunema exiguum Beveridge & Johnson, 1981, pp. 78–80, figs 1–13 (as *exigua*); Beveridge, 1986d, p. 786; Beveridge et al., 1992, p. 365; Griffith et al., 2000, p. 310.

Type data: holotype SAM V1994, allotype SAM V1995, paratypes SAM V1996–2005, BMNH 1980.83–84, USNPC 75749.

Type locality: Tolga, Qld (17° 13′S 145° 29′E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, 2: MG865619 (*Thyl. stigmatica*); ITS2: OM986828 (*Thyl. thetis*, unpublished, SAM voucher no. AHC 49094).

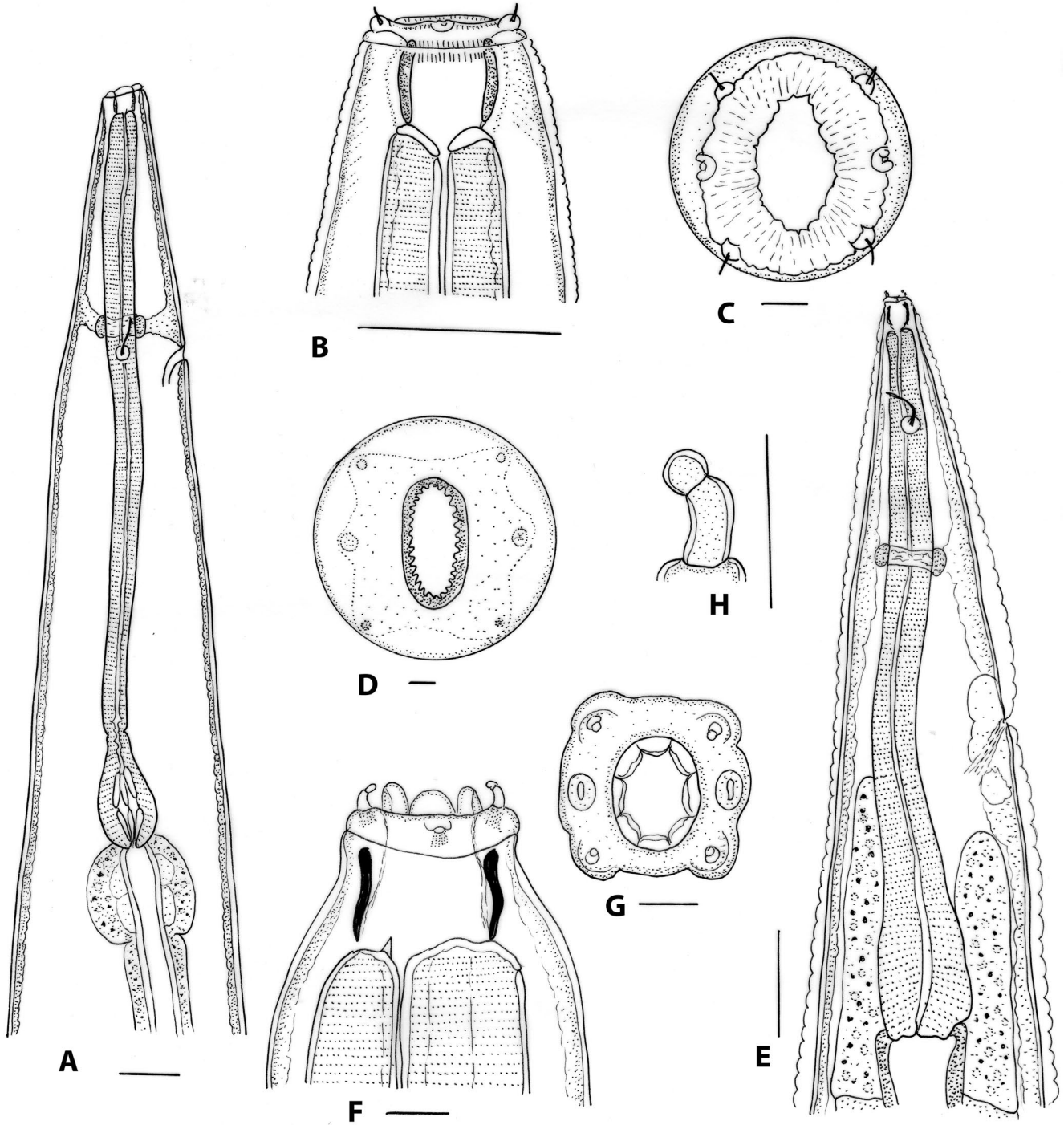


Fig. 2. Genera *Cassunema* and *Cervonemella*. A, *Cassunema exiguum*, anterior end, lateral view; B, *Ca. exiguum*, buccal capsule, lateral view; C, *Ca. exiguum*, anterior end, apical view; D, *Ca. exiguum*, optical transverse section through buccal capsule, at level of longitudinal ridges; E, *Cervonemella reardoni*, anterior end, lateral view; F, *Ce. reardoni*, buccal capsule, lateral view; G, *Ce. reardoni*, anterior end, apical view; H, *Ce. reardoni*, cephalic papilla. (A–D from Beveridge & Johnson, 1981; D–G from Beveridge, 2001).

Scale-bars: A, B, E, 0.1 mm; C, D, F, G, 0.01 mm.

Diagnostic features (Figs 2 A–D): Male 10.9–17.0 mm; female 12.6–20.9 mm; spicules 3.0–3.5 mm; ovejector J-shaped.

Comments: This genus was originally allocated to the Macropostrongylinea by Beveridge & Johnson (1981) based on its poorly sclerotized buccal capsule but was subsequently transferred to the Zoniolaiminea by Beveridge (1986d) based on the structure of the oesophagus. Sequence data suggest that both *Thyl. stigmatica* and *Thyl. thetis* harbour the same species of nematode.

Cervonemella Beveridge, 2001

Type species: *Ce. reardoni* Beveridge, 2001.

Other species: *Ce. kaimanaensis* Dewi & Purwaningsih, 2020.

Generic diagnosis: Cephalic collar present; cephalic papillae bipartite, medially deviated (Fig. 2 H); mouth opening and buccal capsule dorso-ventrally elongate (Fig. 2 G); external leaf crown of 8 elements; buccal capsule as long as wide, walls sclerotized without transverse striations (Fig. 2 F); oesophagus clavate; nerve ring and deirid in anterior oesophageal region; excretory pore in mid-oesophageal region; anterior cells of intestine envelop oesophageal bulb (Fig. 2 E); spicules elongate, alate; gubernaculum present; ovejector J-shaped.

Key to species of *Cervonemella*

1a. Spicules 1.75–2.18 mm; vagina 0.42–0.68 mm . . . . . *Ce. reardoni*

1b. Spicules 2.10–2.86 mm; vagina 1.10–1,22 mm . . . . . *Ce. kaimanaensis*

Cervonemella kaimanaensis Dewi & Purwaningsih, 2020

Cervonemella kaimanaensis Dewi & Purwaningsih, 2020, pp. 541–543, figs 5 A–F.

Type data: holotype, allotype MZB Na 829, paratypes MZB Na 830.

Type locality: Kaimana, Western New Guinea (1° 6′S 130° 51′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea.

Diagnostic features: Males 5.25–7.75 mm; females 6.27–8.74 mm; spicules 2.10–2.86 mm; vagina 1.10–1.22 mm.

Cervonemella reardoni Beveridge, 2001

Cervonemella reardoni Beveridge, 2001, pp. 143–144, figs 1–15.

Type data: holotype SAM AHC 31463, allotype SAM AHC 31464, paratypes SAM AHC 31465, BMNH 2001.4.10.14, USNPC 91143.

Type locality: Usino, Madang, Papua New Guinea (5°13′S 145° 47′E).

Type host: *Dorcopsis hageni* Heller, 1897.

Other hosts: *Dorcopsis luctuosa* (D'Albertis, 1874).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 2 E–H): Males 5.1–6.8 mm; females 6.8–8.9 mm; spicules 1.75–2.18 mm; vagina 0.42–0.68 mm.

Cloacina von Linstow, 1898

Type species: *C. dahli* von Linstow, 1898.

Other species: *C. aedon* Beveridge, 1998; *C. aethra* Beveridge, Jabbar & Shuttleworth, 2014; *C. annulata* Beveridge, 1979; *C. anthea* Beveridge, Jabbar & Shuttleworth, 2014; *C. antigone* Beveridge, 1998; *C. antiope* Beveridge, 1998; *C. ares* Beveridge, 1998; *C. artemis* Beveridge, 1998; *C. asymmetrica* Beveridge, 2019; *C. atthis* Beveridge, 2014; *C. australis* (Yorke & Maplestone, 1926); *C. bancroftorum* Johnston & Mawson, 1939; *C. beveridgei* Dewi & Purwaningsih, 2020; *C. biscoei* Beveridge, 2014; *C. brazellei* Beveridge, 2019; *C. burnettiana* Johnston & Mawson, 1939; *C. caballeroi* Mawson, 1977; *C. cadmus* Beveridge, 1999; *C. caenis* Beveridge, 1998; *C. castor* Beveridge, 1979; *C. celata* Beveridge, 2020; *C. ceres* Beveridge, 1999; *C. chiron* Beveridge, 1999; *C. circe* Beveridge, 1999; *C. cloelia* Beveridge, 1998; *C. clymene* Beveridge, 1998; *C. communis* Johnston & Mawson, 1938; *C. cornuta* (Davey & Wood, 1938); *C. crassicaudata* Beveridge, 2018; *C. cretheis* Beveridge, 2002; *C. cunctabunda* Beveridge, 2002; *C. curta* Johnston & Mawson, 1938; *C. cybele* Beveridge, 1998; *C. daveyi* Mawson, 1977; *C. digitata* Johnston & Mawson, 1940; *C. dindymene* Beveridge, 1998; *C. dirce* Beveridge, 1998; *C. dis* Beveridge, 1998; *C. dryope* Beveridge, 1998; *C. echidne* Beveridge, 1998; *C. edwardsi* Mawson, 1972; *C. eileithyia* Beveridge, 1998; *C. elegans* Johnston & Mawson, 1938; *C. enyo* Beveridge, 1998; *C. eos* Beveridge, 1998; *C. epona* Beveridge, 1998; *C. erigone* Beveridge,

2002; *C. eris* Beveridge, 2018; *C. ernabella* Johnston & Mawson, 1938; *C. eurynome* Beveridge, 2002; *C. expansa* Johnston & Mawson, 1939; *C. feronia* Beveridge, 1998; *C. frequens* Johnston & Mawson, 1938; *C. galatea* Beveridge, Jabbar & Shuttleworth, 2014; *C. gallardi* Johnston & Mawson, 1940; *C. harriganae* Beveridge, 2019; *C. hebe* Beveridge, 1998; *C. hecale* Beveridge, 2002; *C. hecuba* Beveridge, 1998; *C. hera* Beveridge, 1998; *C. herceus* Beveridge, 1998; *C. hermes* Beveridge, 1998; *C. hestia* Beveridge, 1998; *C. hobbsi* Beveridge, 2019; *C. hydriformis* Johnston & Mawson, 1938; *C. hylas* Beveridge, 2019; *C. hyperaea* Beveridge, 2002; *C. hypsipyle* Beveridge, 1998; *C. idas* Beveridge, 2019; *C. inflata* Johnston & Mawson, 1938; *C. io* Beveridge, 1998; *C. ips* Beveridge, 1998; *C. ixion* Beveridge, 1998; *C. johnstoni* Shuttleworth, Jabbar & Beveridge, 2016; *C. kartana* Mawson, 1975; *C. laius* Beveridge, 1999; *C. littoralis* Beveridge, 1998; *C. leto* Beveridge, 1998; *C. liebigi* Johnston & Mawson, 1938; *C. linstowi* Johnston & Mawson, 1940; *C. lityerses* Beveridge, 1998; *C. longelabiata* Johnston & Mawson, 1938; *C. longibursata* Beveridge, 2018; *C. longispiculata* Johnston & Mawson, 1939; *C. macropodis* Johnston & Mawson, 1938; *C. magnipapillata* Johnston & Mawson, 1939; *C. maia* Beveridge, 1998; *C. mawsonae* Beveridge, 1979; *C. metis* Beveridge, 1998; *C. middletoni* Beveridge, 2019; *C. minor* (Davey & Wood, 1938); *C. mundayi* Mawson, 1972; *C. nephele* Beveridge, 2001; *C. nike* Beveridge, 1998; *C. niobe* Beveridge, 1998; *C. obtusa* Johnston & Mawson, 1939; *C. oweni* Beveridge, 2002; *C. papillata* Beveridge, 1979; *C. papillatissima* Beveridge, 1998; *C. papuensis* Beveridge, 2002; *C. parva* Johnston & Mawson, 1938; *C. pearsoni* Mawson, 1971; *C. pelops* Beveridge, 1998; *C. petrogale* Johnston & Mawson, 1938; *C. petronius* Beveridge, 1998; *C. phaeax* Beveridge, 1998; *C. phaedra* Beveridge, 1998; *C. phaethon* Beveridge, 1998; *C. pollux* Beveridge, 1979; *C. polymela* Beveridge, 2002; *C. polyxena* Beveridge, 1998; *C. polyxo* Beveridge, 1998; *C. praxithea* Beveridge, 2002; *C. procris* Beveridge, 2002; *C. ridei* Beveridge, 2014; *C. robertsi* Johnston & Mawson, 1939; *C. sancus* Beveridge & Speare, 1999; *C. sappho* Beveridge & Speare, 1999; *C. schultzi* Beveridge, 2019; *C. sciron* Beveridge & Speare, 1999; *C. selene* Beveridge, 1998; *C. setonicis* Mawson, 1961; *C. similis* Johnston & Mawson, 1939; *C. smalesae* Mawson, 1975; *C. solon* Beveridge & Speare, 1999; *C. solymus* Beveridge & Speare, 1999; *C. spearei* Beveridge, 2018; *C. sterope* Beveridge & Speare, 1999; *C. syphax* Beveridge & Speare, 1999; *C. telemachus* Beveridge, 1999; *C. themis* Beveridge, 1998; *C. theope* Beveridge, 2002; *C. thetidis* Johnston & Mawson, 1939; *C. tyche* Beveridge, 1998; *C. typhon* Beveridge, 1998; *C. tyro* Beveridge, 1998; *C. wallabiae* Johnston & Mawson, 1939; *C. woodi* Beveridge, 2019; *C. woworae* Dewi & Purwaningsih, 2020; *C. xericola* Beveridge, 2018; *C. zetes* Beveridge, 2019.

Species inquirendae:

Cloacina dubia Johnston & Mawson, 1938.

Cloacina inflata Johnston & Mawson, 1938.

Cloacina typica (Johnston & Mawson, 1939)
Syn. *Maplestonema typicum* Johnston & Mawson, 1939; larval stage of *Cloacina* (see Beveridge, 1998a).

Nomina nuda:

Cloacina multipapillata Johnston & Mawson, 1939 in Popova, 1960, p. 31, possible lapsus for *C. magnipapillata* which occurs on the page following that cited by Popova (1960, cited page: 529; actual page 530).

Generic diagnosis: Cephalic collar present; cephalic papillae bipartite; internal leaf crown consisting of 6 or 8, rarely10, petaloid elements originating from full length of buccal capsule; buccal capsule heavily sclerotized, without transverse striations; oesophageal claviform, usually without distinct corpus isthmus and bulb; intestinal lobes absent; bursa without bosses on surface; spicules elongate, alate; gubernaculum usually present; ovejector usually J-shaped, occasionally Y-shaped.

Comments: Neither morphological (Beveridge, 1998a; Beveridge et al., 2002) nor molecular studies (Chilton et al., 2017) have provided any obvious means for dismembering this very large genus. In this review, the key to species has been divided into sections (indicated in bold) based primarily on features of the buccal capsule, the shape and ornamentation of the oesophagus and the shape of the cephalic papillae which are likely to be readily recognisable in lateral views of the anterior extremitities of nematodes and these features are shown primarily in the accompanying illustrations. In some instances, the rays of the dorsal lobe of the bursa and the structure of the vagina provide valuable taxonomic characters and these have been illustrated where appropriate. Perhaps more so than in related genera, numbers of species of *Cloacina* remain undescribed (Beveridge et al., 2014a; Spratt & Beveridge, 2016), suggesting that the key provided here needs to be used with caution.

Key to species of *Cloacina*

Distal segment of cephalic papilla directed medially (Figs 8 F, 9 A, 16 A) . . . . . Section A

Distal segment of cephalic papilla not directed medially . . . . . Section B

Section A
Species with medially directed papillae

1a. Buccal capsule prominently arcuate anteriorly (Fig. 5 I). . . . . *C. circe*
1b. Buccal capsule not prominently arcuate anteriorly 2

2a. Lumen of oesophagus with comb-like structure at level of nerve ring (Fig. 7 P) . . . . *C. edwardsi*
2b. Lumen of oesophagus without comb-like structure at level of nerve ring 3

3a. Oesophageal denticles absent. . . . *C. telemachus*
3b. Oesophageal denticles present (Figs 9 B, G) . . . 4

4a. Oesophageal denticles and deirid at level of nerve ring (Fig. 6 N) . . . . . *C. daveyi*
4b. Oesophageal denticles posterior to nerve ring; deirid anterior to nerve ring 5

5a. Single set of oesophageal denticles present (Fig. 8 P) . . . . . *C. ernabella*
5b. Multiple sets of oesophageal denticles present (Fig. 16 C) 6

6a. Spicules > 1.5 mm . . . . . *C. feronia*
6b. Spicules < 1.2 mm 7

7a. 3–4 sets of oesophageal denticles present . . . . . *C. epona*
7b. More than 4 sets of oesophageal denticles present 8

8a. 5 sets of oesophageal denticles present; vagina Y-shaped . . . . . *C. frequens*
8b.7–8 sets of oesophageal denticles present; vagina J-shaped . . . . . *C. themis*

Section B
With prominent transverse folds in oesophageal corpus (Figs 5 M, 12 M) . . . . . Section B
Without prominent transverse folds in oesophageal corpus . . . . . Section C

1a. Fewer than 10 transverse folds (Fig. 12 M). . . . 2
1b. More than 20 transverse folds (Fig. 5 M) 3

2a. 1–3 sets of oesophageal denticles present; spicules < 2.7 mm (Fig. 15 I) . . . . . *C. similis*
2b. 4 sets of oesophageal denticles present; spicules > 3.0 mm (Fig. 12 O). . . . . *C. niobe*

3a. Distal segment of cephalic papillae globose (Fig. 15K); buccal capsule shallow (length: width ratio = 1.5) (Fig. 15 K) . . . .*C. ridei*
3b. Distal segment of cephalic papillae elongate (Fig. 5 O); buccal not capsule shallow (length: width ratio < 1.2) (Fig. 5 N) 4

4a. Spicules > 3.5 mm; vagina > 1.4 mm . *C. communis*
4b. Spicules < 2.5 mm; vagina < 1.0 mm 5

5a. Spicules > 1.9 mm; spicule ala terminates anterior to tip 6
5b. Spicules < 1.9 mm; spicule ala terminates close to tip 7

6a. Spicule tip ending in 2 blunt lobes; in *Notamacropus parryi* . . . . . *C. phaedra*
6b. Spicule tip simple; in *Notamacropus eugenii* . . . . . *C. phaeax*

7a. 4–5 sets of oesophageal denticles present (Fig. 13 O) . . . . . *C. petrogale*
7b. 2–3 sets of oesophageal denticles present . . . . . *C. petronius*

Section C
Buccal capsule very shallow; length: width ratio > 1 : 4 . . . . . **Section C**
Buccal capsule not shallow; length: width ratio < 1 : 4 . . . . . **Section D**

1a. Anterior margin of buccal capsule with prominent lobes (Figs 9 K, 10 G, 11 H, 12 I). 2
1b. Anterior margin of buccal capsule without prominent lobes 4

2a. Anterior end of body deviated dorsally; oesophagus widest anterior to nerve ring; distal segment of cephalic papilla conical (Figs 14 A, B) . . . . . .*C. polymela*
2b. Anterior end of body straight; oesophagus sub-cylindrical to claviform; distal segment of cephalic papilla globose 3
3a. Spicules < 0.80 mm; vagina Y-shaped . *C. thetidis*
3b. Spicules > 1.90 mm; vagina J-shaped. . . *C. hebe*

4a. Buccal capsule highly sinuous in lateral view (Figs 4 E, 7 R) 5
4b. Buccal capsule straight or very slightly sinuous in lateral view 6

5a. Oesophageal bosses and denticles absent (Fig. 4 D) . . . . . .*C. bancroftorum*
5b. Oesophageal bosses and single, dorsal oesophageal denticle present . . . *C. eileithyia*

6a. Deirid posterior to nerve ring 7
6b. Deirid anterior to nerve ring 8

7a. Oesophageal bosses and denticles absent . . . . . *C. setonicis*
7b. Oesophageal bosses and single, dorsal oesophageal denticle present (Fig. 14 H) .*C. procris*

8a. Oesophageal bosses present 9
8b. Oesophageal bosses absent 10

9a. Oesophagus sub-cylindrical; spicules > 1.0 mm; distal segment of cephalic papilla globose (Fig. 12 T) . . . . . .*C. mundayi*
9b. Oesophagus slender, clavate; spicules < 0.8 mm; distal segment of cephalic papilla conical (Fig. 14 E) . . . . . .*C. polyxo*

10a. Oesophagus sub-cylindrical; distal segment of cephalic papilla ovoid 11
10b. Oesophagus constricted at level of nerve ring; distal segment of cephalic papilla globose (Figs 7 J, K) . . . . . *C. dryope*

11a. Lips present (Fig. 15 A); vagina short, recurrent . . . . . *C. schultzi*
11b. Lips absent (Fig. 12 E); vagina long, straight . . . . . *C. mawsonae*

Section D

Species with an anteriorly arcuate buccal capsule (Figs 3 Q, 10 A) . . . . . Section D
Species with buccal capsule not anteriorly arcuate . . . . . Section E

1a. Cephalic papillae with distal lobe directed medially (Fig. 5 I) . . . . . *C. circe*
1b. Cephalic papillae with distal lobe directed anteriorly 2

2a. Oesophageal bosses absent; proximal segment of cephalic papilla doliiform (Fig. 12 H). 3
2b. Oesophageal bosses present (Figs 10 E, F); proximal segment of cephalic papilla cylindrical 4

3a. Anterior margin of buccal capsule sinuous (Fig. 12 I); proximal segment of cephalic papilla symmetrical (Fig. 12 H) . . . *C. middletoni*
3b. Anterior margin of buccal capsule a regular curve (Fig. 12 S); proximal segment of cephalic papilla asymmetrical (Fig. 12 R) . . . . *C. nephele*

4a. Single dorsal oesophageal denticle present . . . 5
4b. Single dorsal oesophageal denticle absent . . . 6

5a. Spicules > 2.0 mm; buccal capsule moderately arcuate (Figs 10 E, F) . . .*C. hyperaea*
5b. Spicules > 2.0 mm; buccal capsule highly arcuate (Fig. 11 D) . . . . . *C. laius*

6a. Rows of lobes surrounding mouth opening; without comb-like structure in oesophagus (Fig. 3 Q) . . . . . *C. asymmetrica*
6b. No lobes surrounding mouth opening; with comb-like structure in oesophagus, anterior to nerve ring . . . . . .*C. hobbsi*

Section E

Three or four oesophageal denticles present (Fig. 9 G . . . . . Section E
Single dorsal oesophageal denticle present or absent (Figs 4 B, 8 D) . . . . . Section F

1a. Four sets of denticles present posterior to nerve ring (Fig. 9 G) . . . . . *C. gallardi*
1b. Three denticles present at level of nerve ring (Fig. 12 D) 2

2a. Sub-ventral denticles anterior to dorsal denticle (Fig. 11 C) 3
2b. Dorsal denticle anterior to or at same level as sub-ventral denticles (Fig. 12 D) 5

3a. Distal segment of cephalic papilla conical, shorter than proximal segment (Fig. 11 B) 4
3b. Distal segment of cephalic papilla elongate, longer than proximal segment (Fig. 6 M) . . . . *C. dahli*

4a. Dorsal oesophageal tooth prominent; wall of buccal capsule ornamented with numerous v-shaped structures (Fig. 16 H) . . . . . *C. tyche*
4b. Dorsal oesophageal tooth absent; wall of buccal capsule unornamented (Fig. 11 A) . . . . . *C. kartana*

5a. Dorsal denticle anterior to sub-ventrals (Fig. 12 D) 6
5b. Dorsal denticle at approximately same level as sub-ventrals (Fig. 9 Q) 9

6a. Spicules > 3.0 mm; vagina highly sinuous (Fig. 12 B) 7
6b. Spicules < 3.0 mm; vagina straight or very slightly sinuous 8

7a. Distal segment of cephalic papilla ovoid (Fig. 10 O) . . . . . *C. ixion*
7b. Distal segment of cephalic papilla conical (Fig.12 C) . . . . . *C. magnipapillata*

8a. Spicules 1.4–1.7 mm; vagina 0.6–0.8 mm long . . . . . *C. herceus*
8b. Spicules 1.8–2.8 mm; vagina 1.0–1.4 mm long . . . . . *C. pelops*

9a. Deirids at level of nerve ring . . . . . *C. theope*
9b. Deirids in anterior oesophageal region 10

10a. Spicules > 3.5 mm; vagina highly sinuous *C. hera*
10b. Spicules < 2.5 mm; vagina straight or recurrent 11

11a. Spicules 1.9–2.4 mm; female tail swollen, 0.15–0.22 mm long; vagina with prominent flexure (Fig. 9 U) . . . . . *C. hestia*
11b. Spicules 1.1–1.6 mm; female tail slender, 0.28–0.32 mm long; vagina straight (Fig. 9 R) . . . . . *C. hermes*

Section F

Single dorsal oesophageal denticle present (Figs 4 B, 8 P) . . . . . Section F
Single oesophageal denticle absent . . . Section G

1a. Oesophageal bosses present (Figs 10 L, 14 C) . . 2
1b. Oesophageal bosses absent 15

2a. Anterior margin of buccal capsule sinuous (Fig. 7 R) . . . . . *C. eileithyia*
2b. Anterior margin of buccal capsule not sinuous . . 3

3a. Three enlarged bosses present at anterior end of oesophagus (Fig. 4 A) . . . . . *C. australis*
3b. Oesophageal bosses of similar size. 4

4a. Deirid at level of nerve ring or posterior to it. . . 5
4b. Deirid in anterior oesophageal region 6

5a. Buccal capsule symmetrical (Fig. 8 I); oesophageal bosses extend half way to nerve ring . *C. erigone*
5b. Buccal capsule asymmetrical (Fig. 15 R); oesophageal bosses extend to nerve ring . . . . . *C. sterope*

6a. Distal segment of cephalic papilla elongate and cylindrical (Figs 10 K, 12 L) 7
6b. Distal segment of cephalic papilla ovoid or conical, not slender. 9

7a. Spicules < 1.5 mm . . . . . *C. io*
7b. Spicules > 2.0 mm 8

8a. External branchlets of dorsal ray arise at principal bifurcation; vagina with single convolution, mainly straight . . . . . *C. minor*
8b. External branchlets of dorsal ray arise after principal bifurcation; vagina sinuous . . . . *C. tyro*

9a. Spicules > 4.0 mm; vagina spiral (Fig. 7 I) . . *C. dis*
9b. Spicules < 3.0 mm; vagina not spiral 10

10a. Spicules < 1.0 mm . . . . . *C. polyxena*
10b. Spicules > 1.0 mm 11

11a. Buccal capsule asymmetrical; cervical cuticle inflated (Fig. 3 G) . . . . . *C. antigone*
11b. Buccal capsule symmetrical; cervical cuticle not inflated 12

12a. Spicules > 2.5 mm . . . . . *C. leto*
12b. Spicules < 2.5 mm 13

13a. Oesophageal bosses extend to nerve ring . . . . . *C. hecuba*
13b. Oesophageal bosses extend half way to nerve ring 14

14a. Excretory pore posterior to oesophago–intestinal junction; female tail conical . . . . . *C. celata*
14b. Excretory pore in posterior oesophageal region; female tail truncated . . . . . *C. crassicaudata*

15a. Lips present (Figs 7 C, 13 A) 16
15b. Lips absent 17

16a. Cervical cuticle inflated; proximal segment of cephalic papilla bulbous, shorter than distal segment (Fig. 7 C) . . . . . *C. dindymene*
16b. Cervical cuticle not inflated; proximal segment of cephalic papilla cylindrical, longer than distal segment (Fig. 13 A) . . . . . *C. oweni*

17a. Deirid posterior to nerve ring . . . . *C. galatea*
17b. Deirid at level of nerve ring or anterior it . . . 18

18a. Deirid at level of nerve ring 19
18b. Deirid in anterior oesophageal region 20

19a. Anterior margin of buccal capsule arcuate (Fig. 15 D) . . . . . *C. sciron*
19b. Anterior margin of buccal capsule straight (Fig. 8 M) . . . . . *C. eurynome*

20a. Cervical cuticle inflated 21
20b. Cervical cuticle not inflated 23

21a. Cervical inflation shoulder-like; excretory pore well posterior to oesophago-intestinal junction (Fig. 11 S) . . . . . *C. longispiculata*
21b. Cervical inflation not shoulder-like; excretory pore in region of oesophago-intestinal junction. 22

22a. Spicules < 2.0 mm; female tail very short, < 0.20 mm . . . . . *C. cornuta*
22b. Spicules > 3.0 mm; female tail conical, > 0.20 mm . . . . . *C. dirce*

23a. Spicules < 1.80 mm . . . . . *C. idas*
23b. Spicules > 1.80 mm 24

24a. Spicules 1.84–2.26 mm; female tail 0.14–0.22; paired lancets on each sub-ventral lobe of oesophagus (Fig. 13 E) . . . . . *C. papuensis*
24b. Spicules 2.14–2.60 mm; female tail 0.31–0.36; single lancet on each subventral lobe of oesophagus . . . . . *C. spearei*

Section G

Anterior margin of buccal capsule sinuous or forming anterior lobes (Figs 9 K, 11 I, P) . . . Section G
Anterior margin of buccal capsule straight, horizontal . . . . . Section H

1a. Wall of buccal capsule asymmetrical; dorsal wall shorter than ventral wall (Fig. 11 K) 2
1b. Wall of buccal capsule symmetrical 4

2a. Spicules > 2.7 mm; distal segment of cephalic papillae tiny (Fig. 13 R) . . *C. phaethon*
2b. Spicules < 2.6 mm; distal segment of cephalic papillae large, globose (Fig. 11 Q) . . . 3

3a. Spicules 1.2–1.5 mm; vagina straight (Fig. 11 R) . . . . . *C. longelabiata*
3b. Spicules 2.3–2.6 mm; vagina recurrent (Fig. 11 M) . . . . . *C. lityerses*

4a. Cervical cuticle prominently inflated to level of oesophago-intestinal junction (Fig, 3 K) 5
4b. Cervical cuticle not prominently inflated 8

5a. Lips absent; vagina recurrent . . . . . *C. solon*
5b. Lips present; vagina not recurrent 6

6a. Distal segment of cephalic papillae globose, larger than proximal segment . . . . *C. hypsipyle*
6b. Distal segment of cephalic papillae conical, as long as proximal segment 7

7a. Oesophageal bosses present . . . . . *C. aethra*
7b. Oesophageal bosses absent . . . . . *C. artemis*

8a. Lips present 9
8b. Lips absent 11

9a. Excretory pore at level of nerve ring . . . *C. biscoei*
9b. Excretory pore in posterior oesophageal region 10

10a. Buccal capsule in lateral view with anterior margin extending anteriorly to lateral walls (Fig. 16 M); vagina J-shaped . . *C. wallabiae*
10b. Buccal capsule in lateral view with anterior margin at same level as lateral walls (Fig. 12 F); vagina Y-shaped (Fig. 12 G) . . . . . *C. maia*

11a. Buccal capsule arcuate anteriorly (Fig. 12 I) . . . . . *C. middletoni*
11b. Buccal capsule not arcuate anteriorly 12

12a. Oesophagus prominently constricted at nerve ring 13
12b. Oesophagus not prominently constricted at nerve ring 14

13a. Amphids on prominent conical projections (Fig. 14 R) . . . . . *C. sappho*
13b. Amphids not on prominent conical projections . . . . . *C. woworae*

14a. Distal segment of cephalic papilla conical or obtuse, much longer than proximal segment (Fig. 11 H) 15
14b. Distal segment of cephalic papilla conical, shorter than proximal segment (Fig. 15 N) . . 16

15a. Distal segment of cephalic papilla obtuse (Fig.11 H); vagina Y-shaped (Fig. 11 J) . *C. linstowi*
15b. Distal segment of cephalic papilla conical (Fig. 15 T); vagina J-shaped, recurrent arm spiral (Fig.15 U) . . . . . *C. syphax*

16a. Spicules > 3.0 mm; deirids at level of nerve ring . . . . . *C. solymus*
16b. Spicules < 2.0 mm; deirids in anterior oesophageal region. 17

17a. Amphids posterior to cephalic papillae; anterior margin of buccal capsule with prominent lobes (Fig. 14 G) . . . . *C. praxithea*
17b. Amphids not posterior to cephalic papillae; anterior margin of buccal capsule sinuous (Fig. 16 U) . . . . . *C. zetes*

Section H

Buccal capsule asymmetrical in lateral view; dorsal wall shorter or oblique (Figs 3 D, 3 I, 5 G) . . . . . Section H
Buccal capsule symmetrical in lateral view . . . . . Section I

1a. Lips present (Figs 4 J, K) . . . . . *C. caenis*
1b. Lips absent 2

2a. Oesophageal bosses present; spicule tip foot-shaped (Fig. 5 H) . . . . . *C. cloelia*
2b. Oesophageal bosses absent; spicule tip simple. . 3
3a. Peri–oral cuticle prominently lobulated (Fig. 3 I); dorsal oesophageal tooth absent . . . *C. antiope*
3b. Peri–oral cuticle not prominently lobulated (Fig. 3 R); dorsal oesophageal tooth present . . . . . *C. anthea*

Section I

Oesophageal bosses present . . . . . Section I
Oesophageal bosses absent . . . . . Section J

1a. Multiple rows of tiny oesophageal bosses present (Fig. 13 D) . . . . . *C. papillatissima*
1b. Three rows of oesophageal bosses present . . . 2

2a. Deirids posterior to nerve ring. 3
2b. Deirids anterior to nerve ring 6

3a. Lips present (Fig. 5 D) . . . . . *C. ceres*
3b. Lips absent 4

4a. Distal segment of cephalic papilla as long as proximal segment; vagina straight (Fig. 5 A) . . . . . *C. castor*
4b. Distal segment of cephalic papilla much shorter than proximal segment (Fig. 13 B); vagina recurrent (Fig. 8 E) 5

5a. Bosses restricted to anterior oesophageal region . . . . . *C. eos*
5b. Bosses extend to posterior oesophageal region . . . . . *C. papillata*

6a. Spicules > 2.0 mm 7
6b. Spicules < 2.0 mm 9

7a. Lips present (Fig. 13 I) . . . . . *C. parva*
7b. Lips absent 8

8a. Cephalic papillae c. 6 µm long. . . . .*C. johnstoni*
8b. Cephalic papillae c. 12 µm long . . .*C. macropodis*

9a. Distal segment of cephalic papilla as long as proximal segment 10
9b. Distal segment of cephalic papilla much shorter than proximal segment (Fig. 3 F) . . .*C. annulata*

10a. Proximal segment of cephalic papilla cylindrical; cuticle not expanded at level of buccal capsule 11
10b. Proximal segment of cephalic papilla asymmetrically obtuse; cuticular bulge at level of buccal capsule (Fig. 10 D) . . . . *C. hylas*

11a. Dorsal oesophageal and two sub-ventral teeth present . . . . . *C. littoralis*
11b. Dorsal oesophageal and sub-ventral teeth absent . . . . . *C. pollux*

Section J

With prominent lips (Fig. 15 L) . . . . Section J
Without prominent lips . . . . . Section K

1a. Cervical cuticle prominently inflated (Fig. 15 L) . . . . . .*C. smalesae*
1b. Cervical cuticle not prominently inflated 2

2a. Spicules < 4.0 mm . . . . . *C. robertsi*
2b. Spicules > 4.0 mm 3

3a. Spicules < 4.7 mm; ascending vagina with prominent convolutions (Fig. 5 L) . . . *C. clymene*
3b. Spicules > 4.8 mm; ascending vagina without prominent convolutions . . . . . *C. atthis*

Section K

Cervical cuticle prominently inflated (Fig. 7 M, 8 R) . . . . . Section K
Cervical cuticle not prominently inflated . . . . . Section L

1a. Excretory pore well posterior to oesophago-intestinal junction (Fig. 7 M) 2
1b. Excretory pore close to oesophago-intestinal junction. 3

2a. Spicules < 2.0 mm; vagina straight . . . *C. echidne*
2b. Spicules < 5.0 mm; vagina recurrent (Fig. 8 S) . . . . . *C. expansa*

3a. Deirid anterior to nerve ring . . . . . *C. brazellei*
3b. Deirid posterior to nerve ring 4

4a. Distal segment of cephalic papilla much shorter than proximal segment (Fig. 16 O); walls of buccal capsule parallel (Fig. 16 N) . . . . . *C. woodi*
4b. Distal segment of cephalic papilla as long as proximal segment (Fig. 9 I); walls of buccal capsule divergent anteriorly (Fig. 9 H) . . . . . *C. harriganae*

Section L

Deirid at level of or posterior to nerve ring . . . . . Section L
Deirid in anterior oesophageal region . . Section M

1a. Deirid at level of nerve ring (Fig. 3. A) 2
1b. Deirid posterior to nerve ring (Fig. 4 R) 3

2a. Spicules > 3.0 mm; vagina recurrent . . . *C. aedon*
2b. Spicules < 3.0 mm; vagina sinuous. . . . .*C. ares*

3a. External branchlets of dorsal ray arise anterior to major bifurcation (Figs 4 Q, 6 C) 4
3b. External branchlets of dorsal ray arise posterior to major bifurcation 6

4a. Spicules < 2.0 mm; vagina sinuous . . *C. caballeroi*
4b. Spicules < 2.0 mm; vagina spiral or recurrent . . 5

5a. Distal segment of cephalic papilla much shorter than proximal segment (Fig. 6 A); vagina spiral . . . . . *C. cretheis*
5b. Distal segment of cephalic papilla longer than proximal segment; vagina recurrent . *C. beveridgei*

6a. Spicules < 2.0 mm; vagina straight . . . *C. cadmus*
6b. Spicules < 2.0 mm; vagina sinuous 7

7a. Deirid at level of excretory pore; spicule tip minutely bifid; female tail truncated (Fig. 12 J) . . . . . *C. metis*
7b. Deirid between nerve rings and excretory pore (Fig. 8 L); spicule tip simple; female tail conical . . . . . *C. eris*

Section M

1a. Spicules < 1.0 mm 2
1b. Spicules > 1.0 mm 3

2a. External branchlets of dorsal ray arise anterior to principal bifurcation (Fig. 8 B) . . . . *C. enyo*
2b. External branchlets of dorsal ray arise posterior to principal bifurcation . . . . . *C. burnettiana*

3a. Spicules 1.0–2.0 mm 4
3b. Spicules > 2.0 mm 12
4a. Distal segment of cervical papilla ovoid, much longer than cylindrical proximal segment (Fig. 5 E) . . . . . *C. chiron*
4b. Distal segment of cervical papilla conical or cylindrical, as long as or shorter than proximal segment (Fig. 10 N) 5

5a. Dorsal lobe of bursa elongate (Fig. 11 N) 6
5b. Dorsal lobe of bursa similar or slightly longer than lateral lobes 8

6a. External branchlets of dorsal ray arise at or anterior to principal bifurcation (Fig. 6 E) 7
6b. External branchlets of dorsal ray arise posterior to principal bifurcation (Fig. 11 N) . . . . . *C. longibursata*

7a. Dorsal oesophageal tooth present (Fig. 10 M); 8 leaf crown elements; female tail 0.11–0.18 mm . . . . . *C. ips*
7b. Dorsal oesophageal tooth absent (Fig. 6 D); 6 leaf crown elements; female tail 0.35 mm. . . . . *C. cunctabunda*

8a. Distal segment of cephalic papilla ovoid, very small, 1/3 length of proximal segment (Fig. 7 T); buccal capsule striated (Fig. 7 S); vagina recurrent . . . . . *C. elegans*
8b. Distal segment of cephalic papilla one half to as long as proximal segment; buccal capsule not striated; vagina not recurrent. . . . 9

9a. Distal segment of cephalic papilla one half as long as proximal segment . . . . . *C. pearsoni*
9b. Distal segment of cephalic papilla as long as proximal segment (Fig. 10 C) 10

10a. Distal segment of cephalic papilla bulbous, acute at tip (Fig. 10 C) . . . . . *C. hydriformis*
10b. Distal segment of cephalic papilla cylindrical or conical, not, bulbous, rounded at tip (Figs 15 E, 16 J) 11

11a. Spicules 1.10–1.26 mm; 6 leaf crown elements; female tail 0.22–0.30 mm . . . *C. selene*
11b. Spicules 1.30–1.48 mm; 8 leaf crown elements; female tail 0.16–0.21 mm . . *C. typhon*

12a. Vagina recurrent (Fig. 7 B) 13
12b. Vagina not recurrent 16

13a. Spicules < 3.0 mm . . . . . *C. digitata*
13b. Spicules > 3.0 mm 14

14a. Excretory pore posterior to oesophago-intestinal junction . . . . . *C. liebigi*
14b. Excretory pore at level of oesophago-intestinal junction 15

15a. Distal segment of cephalic papilla shorter than proximal segment (Fig. 6 F); descending arm of vagina not sinuous (Fig. 6 G) . . . *C. curta*
15b. Distal segment of cephalic papilla as long as proximal segment (Fig. 16 R); descending arm of vagina sinuous (Fig. 16 S) . . . . . *C. xericola*

16a. Spicules > 3.9 mm . . . . . *C. hecale*
16b. Spicules < 3.5 mm 17

17a. Buccal capsule sinuous in apical views, appearing to have longitudinal ridges in lateral views (Fig. 14 O) . . . . . *C. sancus*
17b. Buccal capsule not sinuous in apical views, without longitudinal ridges in lateral vews . . 18

18a. Spicule tip with prominent ovoid lobe (Fig. 6 H) . . . . . *C. cybele*
18b. Spicule tip simple 19

19a. Walls of buccal capsule slender in lateral view, slightly divergent anteriorly (Fig. 12 Q) . . *C. nike*
19b. Walls of buccal capsule ovoid in lateral view, parallel (Fig. 12 U) . . . . . *C. obtusa*

***Cloacina aedon* Beveridge, 1998**

Cloacina aedon Beveridge, 1998a, pp. 288–290, figs 6–16.
Type data: holotype SAM AHC 26707, allotype SAM AHC 26708, paratypes SAM AHC 7196, BMNH 1996.3.19.1–2, USNPC 86306.
Type locality: Mingela, Qld (19° 53'S 146° 38'E).
Type host: *Lagorchestes conspicillatus* Gould, 1842.
Other hosts: *Onychogalea unguifera* (Gould, 1840).
Site in host: stomach.
Distribution: northern Qld.
Representative DNA sequence data: ITS1, 2: MN86412 (unpublished sequence, morphological voucher specimen SAM AHC 48750).
Diagnostic features (Figs 3 A–C): Males: 9.4–11.5 mm; females 11.7–16.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment much smaller; lips absent; 6 leaf-crown elements; buccal capsule wider than long; anterior margin straight; oesophagus without bosses, denticles and folds; nerve ring and excretory pore in mid-oesophageal region; deirid immediately posterior to nerve ring; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 3.04–3.90 mm; spicule ala terminates anterior to spicule tip; female tail short, conical; vagina recurrent; ovejector J-shaped.
Comments: *Cloacina aedon* was found in six of eight *La. conspicillatus* in north Queensland, but only one of 13 *On. unguifera* in the same region (Beveridge et al., 1992, as *C.* cf. *macropodis*). Additional collections (SAM AHC 32666, 32676, 48750) confirm *L. conspicillatus* as the usual host.

***Cloacina aethra* Beveridge, Jabbar & Shuttleworth, 2014**

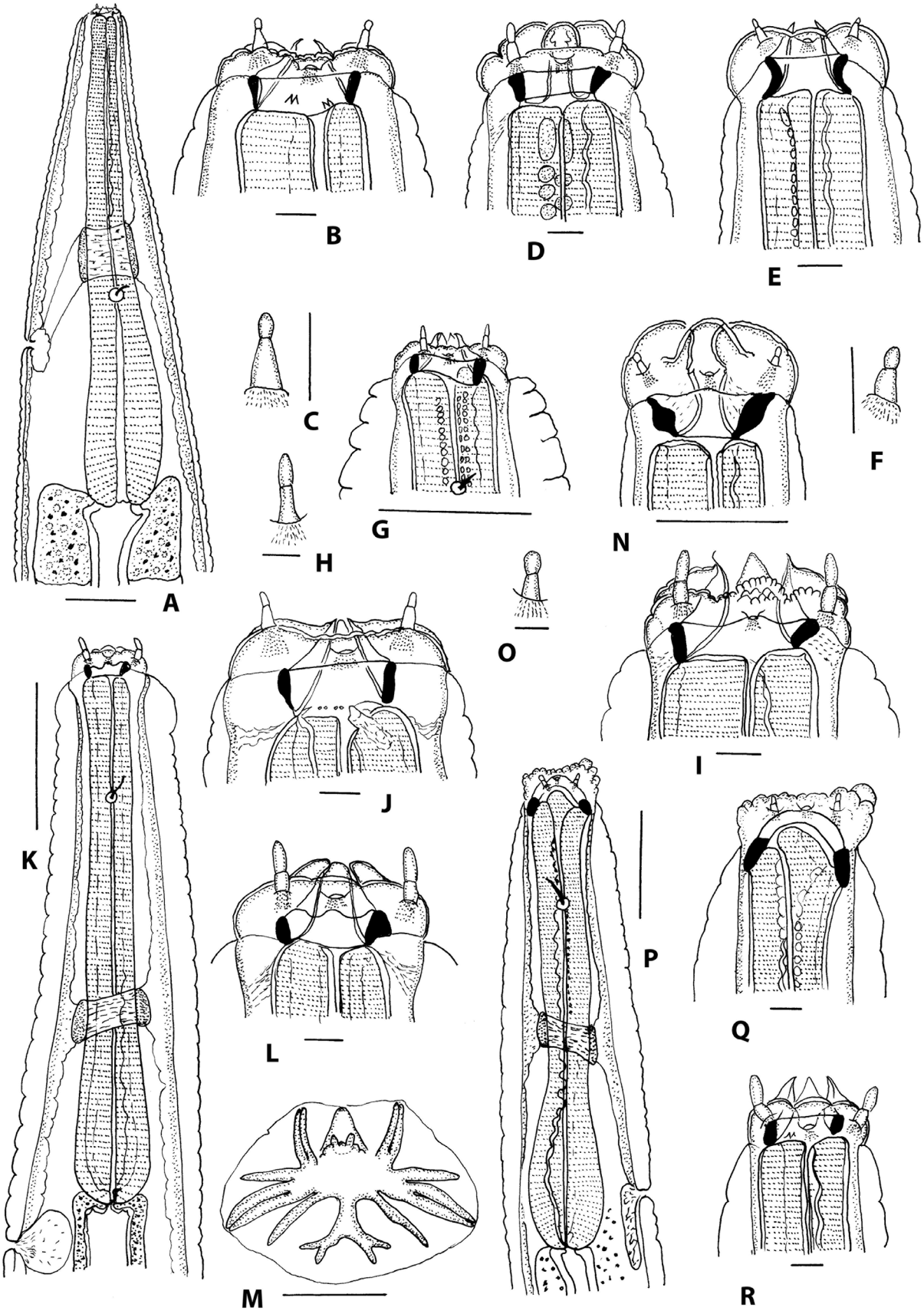
Cloacina aethra Beveridge, Jabbar & Shuttleworth, 2014, pp. 238–240, figs 1–12.
Type data: holotype SAM AHC 46744, allotype SAM AHC 46745, paratypes SAM AHC 46746–7, BMNH 2014.2.4.1–2.
Type locality: Hall's Gap, Vic (37° 08'S 142° 31'E).
Type host: *Wallabia bicolor* (Desmarest, 1804).
Site in host: stomach.
Distribution: Vic. Map: Beveridge et al., 2014, p. 238.
Diagnostic features (Fig. 3 D): Males: 4.3–5.1 mm; females 5.4–5.7 mm; cervical cuticle inflated; cephalic papillae: proximal segment ovoid; distal segment slender, longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long; anterior margin straight in lateral views, undulate in dorso-ventral views; oesophagus with bosses extending to level of nerve ring, denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 1.01–1.13 mm; spicule ala diminishes gradually to spicule tip; female tail slender, conical; vagina straight; ovejector J-shaped.
Comments: This species is restricted to *Wal. bicolor* in Victoria.

***Clocina annulata* Beveridge, 1979**

Clocina annulata Beveridge, 1979, pp. 369–372, figs 25–32; Beveridge et al., 1985, p. 378; Beveridge, 1998a, pp. 290–292, figs 17–27; Aussavy et al., 2011, p. 17; Shuttleworth et al., 2014, p. 263; Vendl & Beveridge, 2014, p. 109; Spratt et al., 2017, p. 242.
Type data: holotype SAM V1645, allotytpe SAM V1646, paratypes SAM V1647–50.
Type locality: Bellbird Creek, Vic (37° 40'S 148° 49').
Type host: *Wallabia bicolor* (Desmarest, 1804).
Other hosts: *Notamacropus parma* (Waterhouse, 1846).
Site in host: stomach.
Distribution: Qld, NSW, Vic.
Representative DNA sequence data: ITS1, 2: KM21983–40, KM219923–4.
Diagnostic features (Figs 3 E, F): Males: 3.7–4.5 mm; females 3.9–5.2 mm; cervical cuticle very slightly inflated; cephalic papillae: proximal segment conical;

Fig. 3. Genus *Cloacina*. A, *Cloacina aedon*, anterior end, lateral view; B, *C. aedon,* buccal capsule, lateral view; C, *C. aedon,* cephalic papilla; D, *Cloacina aethra*, buccal capsule, lateral view; E, *Cloacina annulata*, buccal capsule, lateral view; F, *C. annulata,* cephalic papilla; G, *Cloacina antigone,* buccal capsule, lateral view; H, *C. antigone,* cephalic papilla; I, *Cloacina antiope*, buccal capsule, lateral view; J, *Cloacina ares*, buccal capsule, lateral view; K, *Cloacina artemis*, anterior end, lateral view; L, *C. artemis*, buccal capsule, lateral view; M, *C. artemis*, bursa, apical view; N, *Cloacina atthis,* buccal capsule, lateral view; O, *C. atthis,* cephalic papilla; P, *Cloacina asymmetrica*, anterior end, lateral view; Q, *C. asymmetrica*, buccal capsule, lateral view; R, *Cloacina anthea*, buccal capsule, lateral view. (A–C, E–M from Beveridge, 1998a; D, R from Beveridge et al., 2014a; N, O, from Beveridge et al., 2014b; P, Q, from Beveridge et al., 2019).

Scale-bars: A, G, K, M, N, P, 0.1 mm; B–F, H–J, L, O, Q, R, 0.01 mm.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distal segment ovoid, much shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin straight in lateral views, walls incurved; oesophagus with bosses extending to level of nerve ring, denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 0.86–1.05 mm; spicule ala terminates abruptly anterior to spicule tip; female tail slender, conical; vagina straight; ovejector J-shaped.

Comments: *Cloacina annulata* is a common parasite of *Wal. bicolor* (Beveridge, 2016) with only a single record from *N. parma*. Shuttleworth et al. (2014) noted some genetic differences between Victorian and Queensland specimens.

***Cloacina anthea* Beveridge, Jabbar & Shuttleworth, 2014**

Cloacina anthea Beveridge, Jabbar & Shuttleworth, 2014, pp. 241–243, figs 13–22.

Type data: holotype SAM AHC 46732, allotype SAM AHC 46733, paratypes SAM AHC 46734, BMNH 2014.2.4.3–4.

Type locality: Charters Towers, Qld (20° 05′S 146° 16′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: northern Qld, Vic. Map: Beveridge et al., 2014, p. 238.

Diagnostic features (Fig. 3 D): Males 4.1–4.8 mm; females 4.8–5.3 mm; cervical cuticle inflated; cephalic papillae: proximal segment doliiform; distal segment ovoidal, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral views; dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses, denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; dorsal lobe of bursa longer than remaining lobes; external branchlets of dorsal ray shorter than internal branchlets; spicules 0.70–0.76 mm; spicule ala diminishes gradually to spicule tip; female tail conical; vagina straight; ovejector J-shaped.

Comments: Although restricted to *Wal. bicolor*, this species has an unusual distribution with several collections in Victoria and an outlying collection in north Queensland.

***Cloacina antigone* Beveridge, 1998**

Cloacina antigone Beveridge, 1998a, pp. 292–294, figs 28–41; Beveridge et al., 1998, p. 484; Beveridge, 2016, p. 212.

Type data: holotype SAM AHC 26830, allotype SAM AHC 26831, paratypes SAM AHC13639, 26832, BMNH 1996.3.19.3–6, USNPC 86361.

Type locality: Charters Towers, Qld (20° 05′S 146° 16′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Other hosts: *Notamacropus agilis* (Gould, 1842); *Notamacropus dorsalis* (Gray, 1837); *Lagorchestes conspicillatus* Gould, 1842.

Site in host: stomach.

Distribution: central and northern Qld.

Representative DNA sequence data: ITS1, 2: MF284674.

Diagnostic features (Figs 3 G, H): Males 4.8–6.7 mm; females 5.9–8.8 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment tapering, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long; asymmetrical, deeper on dorsal side; anterior margin sinuous in lateral views; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring; single dorsal denticle anterior to nerve ring; oesophageal folds absent; nerve ring in mid-oesophageal region; excretory pore near oesophago-intestinal junction; deirid in anterior oesophageal region; dorsal lobe of bursa no longer than remaining lobes; external branchlets of dorsal ray shorter than internal branchlets; spicules 1.85–2.22 mm; spicule ala diminishes gradually to spicule tip; female tail conical; distal vagina straight, slightly convoluted at entry to ovejector; ovejector J-shaped.

Comments: *Cloacina antigone* was found to be almost equally prevalent in *N. dorsalis* and *Wal. bicolor* in northern Queensland (Beveridge et al., 1998). The record from *La. conspicillatus* is based on the collection of one male from a single host (SAM AHC 24670). The record from *N. agilis* (SAM AHC 26765) was not included by Speare et al. (1983) although the host animal was clearly part of their collection. It was included by Beveridge et al. (1998), but not by Beveridge (1998a). The presence of specimens in SAM confirm the record, but it was reported at a prevalence of only 3% in this host species by Beveridge et al. (1998).

***Cloacina antiope* Beveridge, 1998**

Cloacina antiope Beveridge, 1998a, pp. 294–296, figs 42–51; Beveridge et al., 1998, p. 484.

Type data: holotype SAM AHC 26715, allotype SAM AHC 26716, paratypes SAM AHC 26717–8.
Type locality: Logan Village, Qld (27° 46′S 153° 06′E).
Type host: *Notamacropus dorsalis* (Gray, 1837).
Site in host: stomach.
Distribution: eastern Qld.
Diagnostic features (Fig. 3 I): Males: 3.6–4.4 mm; females 3.4–5.9 mm; cervical cuticle inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; peri-oral cuticle inflated and lobed; buccal capsule wider than long, asymmetrical with dorsal wall obliquely oriented in lateral views; anterior margin slightly sinuous in lateral views; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray short; spicules 0.90–1.13 mm; spicule ala diminishes gradually anterior to spicule tip; female tail slender, conical; vagina short, straight; ovejector J-shaped.
Comments: *Cloacina antiope* is the only species, apart from *C. asymmetrica*, with the peri-oral cuticle inflated and lobed. It is known only from *N. dorsalis* from Queensland.

***Cloacina ares* Beveridge, 1998**

Cloacina ares Beveridge, 1998a, pp. 296–298, figs 52–64; Beveridge, 2018, p. 202; 2020e, p. 204.
Type data: holotype SAM AHC 26709, allotype SAM AHC 26710, paratypes SAM AHC 26711.
Type locality: Cunnamulla, Qld (28° 04′S 145° 41′E).
Type host: *Osphranter rufus* (Desmarest, 1822).
Other hosts: *Wallabia bicolor* (Desmarest, 1804).
Site in host: stomach.
Distribution: Qld, NSW.
Diagnostic features (Fig. 3 J): Males: 6.6–10.3 mm; females 9.9–13.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, much shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin straight in lateral views; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid at level of nerve ring; bursal lobes of equal length; external branchlets of dorsal ray arising at or immediately after principal bifurcation; spicules 2.3–3.0 mm; spicule ala terminates abruptly anterior to spicule tip; female tail slender, conical; vagina convoluted; ovejector J-shaped.
Comments: *Cloacina ares* appears to be relatively uncommon in *O. rufus* and is restricted to eastern Australia but is distinguished from congeners in this host by the position of the deirid. The single record from *Wal. bicolor* is from the north–east of New South Wales. A very similar species, *C. eris*, also from *O. rufus*, differing primarily in the position of the deirid occurs mainly in Western Australia with one occurrence in north-western Queensland, in sympatry with *C. ares* (Beveridge, 2018).

***Cloacina artemis* Beveridge, 1998**

Cloacina artemis Beveridge, 1998a, pp. 298–301, figs 65–75; Beveridge et al., 1998, p. 484; Webley et al., 2004, p. 629; Aussavy et al., 2011, p. 14, 15; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 240.
Type data: holotype SAM AHC 26712, allotype SAM AHC 26713, paratypes SAM AHC 26714, 27358–60, BMNH 1996.3.19.7–8, USNPC 86362 (as 8P6362).
Type locality: Nagambie, Vic. (36° 47′S 145° 10′E).
Type host: *Macropus giganteus* Shaw, 1790.
Other hosts: *Macropus fuliginosus* (Desmarest, 1817); *Lagorchestes conspicillatus* Gould, 1842.
Site in host: stomach.
Distribution: Qld, NSW, Vic, SA.
Diagnostic features (Figs 3 K–M): Males: 6.2–7.5 mm; females 7.8–10.5 mm; cervical cuticle inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, much longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin sinuous in lateral views; oesophagus without bosses, denticles and folds; nerve ring in posterior-oesophageal region; excretory pore near oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray short; spicules 1.6–1.9 mm; spicule ala terminates abruptly anterior to spicule tip; female tail slender, conical; vagina sinuous; ovejector J-shaped.
Comments: This species is common in both *Mac. fuliginosus* and *Mac. giganteus* virtually throughout their geographical ranges. Specimens held in SAM indicate that the range includes *Mac. giganteus* in Tasmania (AHC 24578) and *Mac. fuliginosus* south of Perth (AHC 31870, 31889). The single record from *La. conspicillatus* consists of one male nematode recovered from eight hosts examined in north Queensland (Beveridge et al., 1992) (SAM AHC 12324).

***Cloacina asymmetrica* Beveridge, 2019**

Cloacina asymmetrica Beveridge, 2019 in Beveridge et al., 2019, pp. 455–457, figs 1–13.

Type data: holotype SAM AHC 48258, allotype SAM AHC 48259, paratypes SAM AHC 48260.

Type locality: Collie, WA (33° 22'S 116° 09'E).

Type host: *Notamacropus irma* (Jourdan, 1837).

Site in host: stomach.

Distribution: south-western WA.

Representative DNA sequence data: ITS1, 2: MK573549, 373545.

Diagnostic features (Figs 3 P, Q): Males 3.2–4.4 mm; females 3.4–5.3 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips absent; cephalic collar asymmetrical, larger on ventral aspect, prominently lobed; 6 leaf-crown elements; buccal capsule dorso-ventrally elongate, arcuate anteriorly, walls ring-like; slightly asymmetrical, deeper on ventral side; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring; denticles and oesophageal folds absent; nerve ring in mid-oesophageal region; excretory pore near oesophago-intestinal junction; deirid in anterior oesophageal region; dorsal lobe of bursa no longer than remaining lobes; external branchlets of dorsal ray short; spicules 1.43–1.70 mm; spicule ala diminishes gradually to spicule tip; female tail conical; vagina straight; ovejector J-shaped.

Comments: This is a highly distinctive species with its arcuate buccal capsule and asymmetrical cephalic collar. It is found only in *N. irma* in the south west of Western Australia.

***Cloacina atthis* Beveridge, 2014**

Cloacina atthis Beveridge, 2014 in Beveridge et al., 2014b, pp. 3487–3490, figs 1–13.

Type data: holotype WAM V8240, allotype WAM V8241, paratypes WAM V8242, SAM AHC 45945, BMNH 2014.4.14.1–2.

Type locality: 57 km N of the Fortescue River Roadhouse, WA (21° 17'S 116° 08'E).

Type host: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: WA (Pilbara Region). Map: Beveridge et al., 2014b, p. 3490.

Representative DNA sequence data: ITS1, 2: KM016823, 016826, 016832, KU853903.

Diagnostic features (Figs 3 N, O): Males 13.4–16.4 mm; females 21.2–23.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, slightly shorter than proximal segment; lips prominent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin slightly undulating in lateral views, walls thickest in mid-region, tapering at both ends, directed anterolaterally; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branches of dorsal ray short; spicules 4.00–4.63 mm; spicule tip bifid; spicule ala diminishes gradually to spicule tip; female tail conical; distal vagina straight; anterior vagina recurrent; ovejector J-shaped.

Comments: *Cloacina atthis* is most similar to *C. clymene*. However, there are minor morphological differences as well as substantial differences in DNA sequence data. In addition, they are not closely related phylogenetically (Chilton et al., 2017). While *C. atthis* is limited to the Pilbara region of Western Australia, *C. clymene* occurs in the same host species mainly along the east coast of Australia.

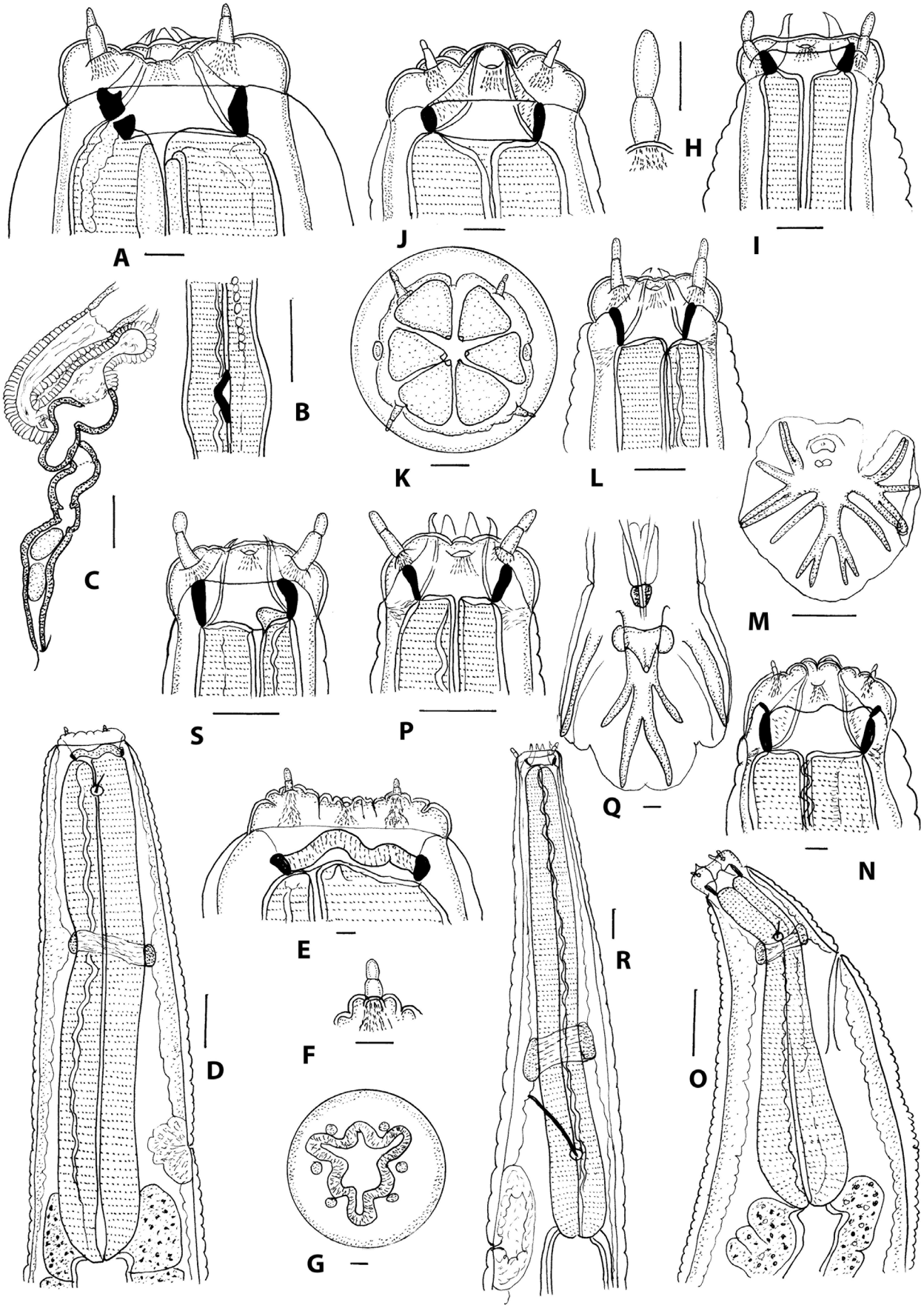
***Cloacina australis* (Yorke & Maplestone, 1926)**

Macropostrongylus australis Yorke & Maplestone, 1926, p. 75, fig. 41; Skrjabin et al., 1952, p. 291; Popova, 1958, p. 261, fig. 177; Yamaguti, 1961, p. 385.

Cloacina australis: Mawson, 1977b, p. 51; Speare et al., 1983, p. 90; Begg et al., 1995, p. 47; Beveridge, 1998a,

Fig. 4. Genus *Cloacina*. A, *Cloacina australis*, buccal capsule, lateral view; B, *C. australis*, oesophageal denticle, lateral view; C, *C. australis*, vagina, lateral view; D, *Cloacina bancroftorum*, anterior end, lateral view; E, *C. bancroftorum*, buccal capsule, lateral view; F, *C. bancroftorum*, cephalic papilla; G, *C. bancroftorum*, optical transverse section through buccal capsule; H, *Cloacina brazellei*, cephalic papilla; I, *C. brazellei*, buccal capsule, lateral view; J, *Cloacina caenis*, buccal capsule, lateral view; K, *C. caenis*, anterior end, apical view showing six lips; L, *Cloacina burnettiana*, buccal capsule, lateral view; M, *Cloacina biscoei*, bursa, apical view showing origin of externo-dorsal ray from the dorsal trunk; N, *C. biscoei*, buccal capsule, lateral view; O, *C. biscoei*, anterior end, lateral view showing excretory pore at level of nerve ring; P, *Cloacina caballeroi*, buccal capsule, lateral view; Q, *C. caballeroi*, dorsal lobe of bursa and dorsal ray; R, *C. caballeroi*, anterior end, lateral view, with posterior deirid; S, *Cloacina cadmus*, buccal capsule, lateral view. (A–G, J–L, P–R, from Beveridge 1998a; H, I, from Beveridge et al., 2019; M–O, from Beveridge, 2014; S, from Beveridge, 1999b).

Scale-bars: C, D, M, O, R, 0.1 mm; A, B, E–L, N, P, Q, 0.01 mm.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pp. 301–303, figs 76–89; Beveridge et al., 1998, p. 484.
Type data: syntypes BMNH 1927.7.21.4–8.
Type locality: Townsville, Qld (19° 15′S 146° 49′E).
Type host: *Notamacropus agilis* (Gould, 1842).
Other hosts: *Aepyprymnus rufescens* (Gray, 1837); *Macropus giganteus* Shaw, 1790; *Notamacropus parryi* (Bennett, 1835); *Petrogale persephone* Maynes, 1982.
Site in host: stomach.
Distribution: PNG, Qld, NT (Top End).
Diagnostic features (Figs 4 A–C): Males 7.2–8.7 mm; females 7.4–9.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, much shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral views, walls thickest in mid-region; prominent, rounded oesophageal tooth projects into buccal capsule; anterior extremity of oesophagus with 3 prominent, elongate, sclerotized structures; oesophagus with bosses extending almost to nerve ring, single dorsal denticle present; folds absent; nerve ring in mid–oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 2.4–2.9 mm; spicule ala diminishes gradually to spicule tip; female tail conical; vagina convoluted; ovejector J-shaped.
Comments: The principal host of *C. australis* appears to be *N. agilis* although where it is in sympatry with *N. parryi*, the parasite is also common in the latter host (Beveridge et al., 1998). *Aepyprymnus rufescens*, *Mac. giganteus* and *Pet. persephone* appear to be incidental hosts. Collections in SAM (AHC 24705, 25766–7) indicate that the species extends into the Northern Territory in *N. agilis*.

***Cloacina bancroftorum* Johnston & Mawson, 1939**
Cloacina bancroftorum Johnston & Mawson, 1939a, p. 133, figs 29–33; 1939b, pp. 514, 533; Skrjabin et al., 1952, p.160; Popova 1960, p. 12; Mawson, 1961b, p. 86; Yamaguti, 1961, p. 400; Beveridge, 1998a, pp. 303–306, figs 90–100; Beveridge et al., 1998, p. 484.
Type data: holotype and allotype SAM V1551.
Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).
Type host: *Notamacropus dorsalis* (Gray, 1837).
Site in host: stomach.
Distribution: eastern Qld.
Representative DNA sequence data: ITS1, 2: MF284675.
Diagnostic features (Figs 4 D–G): Males 7.5–10.1 mm; females 8.6–13.6 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, slightly longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, ringlike, asymmetrical; buccal capsule undulate in lateral view, sinuous in apical view; oesophagus sub-cylindrical without bosses denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 4.98–5.75 mm; spicule ala diminishes gradually to spicule tip; female tail conical; vagina convoluted, recurrent; ovejector J-shaped.
Comments: This species is a common parasite of *N. dorsalis* in Queensland and is unique with its shallow, highly sinuous buccal capsule. Johnston & Mawson (1939b) also reported it from *Thyl. thetis*, but this appears to be a case of mistaken host identification (Beveridge, 1998a).

***Cloacina beveridgei* Dewi & Purwaningsih, 2020**
Cloacina beveridgei Dewi & Purwaningsih, 2020, pp. 539–541, figs 3–4.
Type data: holotype, allotype MZB Na827, paratypes MZB Na828.
Type locality: Kaimana District, Western New Guinea (1° 6′S 130° 51′E).
Type host: *Dorcopsis muelleri* (Schlegel, 1866).
Site in host: stomach.
Distribution: Western New Guinea .
Diagnostic features: Males 3.9–6.4 mm; females 5.0–6.4 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much longer than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule much wider than long, symmetrical; anterior margin slightly undulating in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid–oesophageal region; excretory pore in posterior oesophageal region; deirid between nerve ring and excretory pore; bursal lobes of equal length; external branchlets of dorsal ray arise prior to principal bifurcation; spicules 2.0–2.4 mm; spicule ala diminishes gradually to spicule tip; female tail conical; distal vagina straight; anterior vagina recurrent; ovejector J-shaped.
Comments: This species belongs to a small group, mainly from Papua New Guinea, in which the external branchlets of the dorsal ray arise anterior to the principal bifurcation.

***Cloacina biscoei* Beveridge, 2014**

Cloacina biscoei Beveridge, 2014, pp. 252–254, figs 14–25.

Type data: holotype SAM AHC 46970, allotype SAM AHC 46971, paratypes SAM AHC 46972.

Type locality: Wedge Point, Bernier Island, WA (24° 47′S 113° 09′E).

Type host: *Lagostrophus fasciatus* (Péron & Lesueur, 1807).

Site in host: stomach.

Distribution: WA.

Diagnostic features (Figs 4 M–O): Males 3.5–4.4 mm; females 5.6–7.1 mm; cervical cuticle not inflated; cephalic papillae tiny: proximal segment trapezoidal; distal segment ovoid, as long as proximal segment; lips present; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin undulating in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in anterior oesophageal region; deirid at level of nerve ring; excretory pore at level of nerve ring; dorsal lobe of bursa elongate; externo-dorsal ray arises from dorsal trunk; external branchlets of dorsal ray short; spicules 1.4–1.6 mm; spicule ala diminishes gradually to spicule tip; spicule tip sharp; female tail conical; vagina short, straight; ovejector J-shaped.

Comments: This species, along with *C. ridei* from the same host, shares the unusual features of the externo-dorsal ray arising from the dorsal trunk and an anteriorly placed excretory pore.

***Cloacina brazellei* Beveridge, 2019**

Cloacina brazellei Beveridge, 2019 in Beveridge et al., 2019, pp. 457–460, figs 14–26.

Type data: holotype SAM AHC 48273, allotype SAM AHC 48274, paratypes SAM AHC 48275.

Type locality: 80 km N of Williams, WA (33° 02′S 116° 53′E).

Type host: *Notamacropus irma* (Jourdan, 1837).

Other hosts: *Setonix brachyurus* (Quoy & Gaimard, 1830).

Site in host: stomach.

Distribution: south-western WA.

Representative DNA sequence data: ITS1, 2: MK573552, 573551.

Diagnostic features (Figs 4 H, I, 44 B): Males: 3.0–3.7 mm; females 3.3–4.5 mm; cervical cuticle prominently inflated to level of oesophago-intestinal junction; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral views; dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray short; spicules 0.90–1.10 mm; spicule ala diminishes gradually to spicule tip; female tail long, slender; vagina straight; ovejector J-shaped.

Comments: A small species apparently common in *N. irma* in south–western Australia, with a single collection from the sympatric host species, *Set. brachyurus*.

***Cloacina burnettiana* Johnston & Mawson, 1939**

Cloacina burnettiana Johnston & Mawson, 1939a, pp. 130–131, figs 20–22; Yamaguti, 1961, p. 400; Beveridge, 1998a, pp. 306–308, figs 101–114; Beveridge et al., 1998, p. 484.

Type data: holotype and allotype SAM V1548.

Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Other hosts: *Notamacropus parma* (Waterhouse, 1846).

Site in host: stomach.

Distribution: eastern Qld; north-eastern NSW.

Representative DNA sequence data: ITS1, 2: MF284676.

Diagnostic features (Fig. 4 L): Males: 2.7–4.1 mm; females 3.0–5.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid–oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray short; spicules 0.60–0.70 mm; spicule tip bifid; spicule ala terminates in enlarged flange at spicule tip; female tail slender, conical; vagina straight; ovejector J-shaped.

Comments: The specimens from *N. parma* differ slightly from those found in *N. dorsalis* in the size of the cephalic papillae and the width of the buccal capsule (Beveridge, 1998a) and their status should be reviewed if additional material from this host species become available.

***Cloacina caballeroi* Mawson, 1977**

Cloacina caballeroi Mawson, 1977c, pp. 456–458, figs 5–9; Beveridge, 1998a, pp. 308–310, figs 115–121; Beveridge, 2002b, p. 2.

Type data: holotype BBM HT39, allotype BBM HT40, paratypes SAM AHC 6388.
Type locality: Geelvink Bay, Western New Guinea (2° 30′S 135° 20′E).
Type host: *Dorcopsis muelleri* (Shlegel, 1866).
Other hosts: *Dorcopsis luctuosa* (D'Albertis, 1874); *Dorcopsis hageni* Heller, 1897.
Site in host: stomach.
Distribution: PNG, Western New Guinea.
Diagnostic features (Figs 4 P–R): Males: 3.5–3.6 mm; females 3.2–3.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in posterior oesophageal region; excretory pore at oesophago-intestinal junction; deirid very long, in posterior oesophageal region; dorsal lobe of bursa of elongate; external branchlets of dorsal ray short, arise anterior to principal bifurcation; spicules 1.23–1.45 mm; female tail conical; vagina straight, reflexed at entry to ovejector; ovejector J-shaped.
Comments: This species is readily recognisable from the shape of the dorsal ray and the position of the deirid. However, the details of its spicule morphology are incomplete.

***Cloacina cadmus* Beveridge, 1999**

Cloacina cadmus Beveridge, 1999b, pp. 24, 26–27, figs 52–62.
Type data: holotype SAM AHC 30555, allotype SAM AHC 30556, paratypes SAM AHC 30557, BMNH 1998.9.28.1–2.
Type locality: Rottnest Island, WA (31° 59′S 115° 31′E).
Type host: *Setonix brachyurus* (Quoy & Gaimard, 1830).
Site in host: stomach.
Distribution: south-western WA.
Representative DNA sequence data: ITS1, 2: MF284677.
Diagnostic features (Fig. 4 S): Males: 3.4–4.7 mm; females 3.9–5.3 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in posterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray short; spicules 1.31–1.46 mm; spicule tip bifid; spicule ala terminates abruptly anterior to spicule tip, continued by flange surrounding tip; female tail conical; vagina long, straight; ovejector J-shaped.

***Cloacina caenis* Beveridge, 1998**

Cloacina caenis Beveridge, 1998a, pp. 310–313, figs 122–134; Bradley et al., 2000, p. 39.
Type data: holotype SAM AHC 26836, allotype SAM AHC 26837, paratypes SAM 26838, 27374, BMNH 1996.3.19.14–15, USNPC 86364.
Type locality: Expedition Creek, Blue Range, Qld (19° 04′S 154° 31′E).
Type host: *Petrogale assimilis* Ramsay, 1877.
Other hosts: *Petrogale brachyotis* (Gould, 1841); *Petrogale coenensis* Eldridge & Close, 1992; *Petrogale godmani* Thomas, 1923; *Petrogale herberti* Thomas, 1926; *Petrogale inornata* Gould, 1842; *Petrogale lateralis* Gould, 1840; *Petrogale mareeba* Eldridge & Close, 1992; *Petrogale purpureicollis* Le Souef, 1924; *Petrogale sharmani* Eldridge & Close, 1992; *Petrogale wilkinsi* Thomas, 1926; *Petrogale xanthopus* Gray,1855.
Site in host: stomach.
Distribution: NT, Qld, SA.
Representative DNA sequence data: ITS1, 2: FM992588, 992591–5; cox1 KJ851923–5; 18S, 28S, ITS: KJ776343–5.
Diagnostic features (Figs 4 J, K): Males: 4.6–5.5 mm; females 5.3–7.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much shorter than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray short; spicules 1.00–1.45 mm; female tail conical; vagina short, straight; ovejector J-shaped.
Comments: Although found in a wide range of species of rock wallabies (*Petrogale* spp.), details of the spicule tips of this species remain to be described. A molecular study using material from *Pet. assimilis*, *Pet. herberti*, *Pet. inornata*, *Pet. mareeba* and *Pet. purpureicollis* (Chilton et al., 2009a) suggests the possibility that *C. caenis* may be a complex of multiple species.

***Cloacina castor* Beveridge, 1979**

Cloacina castor Beveridge, 1979, pp. 372–374, figs 33–41; Beveridge et al., 1985, p. 378; Beveridge, 1998a, pp. 313–315, figs 135–145; Beveridge et al., 1998, p. 484; Aussavy et al., 2011, p. 17; Vendl & Beveridge, 2014, p. 109; Shuttleworth et al., 2014, p. 263; Beveridge, 2016, p. 212; Spratt et al., 2017, p. 242.

Type data: holotype SAM V1651.

Type locality: Teesdale, Vic (38° 02′S 144° 03′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: Qld, NSW, Vic.

Representative DNA sequence data: ITS1, 2: KM219841, 219925.

Diagnostic features (Fig. 5 A): Males: 3.6–4.6 mm; females 3.2–4.8 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, as long as proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral view; dorsal oesophageal tooth present; oesophagus with bosses extending almost to nerve ring, denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in posterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray arise at principal bifurcation; spicules 1.10–1.38 mm; spicule tip bifid; ala diminishes in width, forms flange around tip; female tail elongate; vagina straight; ovejector J-shaped.

Comments: *Cloacina castor* occurs throughout the geographical range of its host, *Wal. bicolor*, but is not abundant (Beveridge, 2016).

***Cloacina celata* Beveridge, 2020**

Cloacina celata Beveridge, 2020f, pp. 215–223, figs 1 A–M.

Type data: holotype QM G238391, allotype QM G238392, paratypes QM G238292–5, SAM AHC 49058.

Type locality: Forty Mile Scrub National Park, Qld (18º 05′S 144º 51′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

Distribution: north-eastern Qld.

Diagnostic features (Figs 5 C–D): Males: 4.2–5.2 mm; females 4.3–6.3 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending half way to nerve ring; single dorsal denticle present; folds absent; nerve ring in mid-oesophageal region; excretory pore well posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray shorter than internal branchlets; spicules 1.55–2.05 mm; spicule tip blunt; ala diminishes in width to tip; female tail conical; vagina convoluted; ovejector J-shaped.

Comments: *Cloacina celata* was not found in 39 *N. dorsalis* reported by Beveridge et al. (1998). In the single host specimen from which it is known, it constituted approximately 1% of the estimated 5,000 nematodes present (Beveridge, 2020f). Its low abundance may be the reason it has been overlooked in the past.

***Cloacina ceres* Beveridge, 1999**

Cloacina ceres Beveridge, 1999b, pp. 18–20, figs 1–14.

Type data: holotype SAM AHC 30558, allotype SAM AHC 30559, paratypes SAM AHC 30560, BMNH 1998.9.28.3–4.

Type locality: Rottnest Island, WA (31° 59′S 115° 31′E).

Type host: *Setonix brachyurus* (Quoy & Gaimard, 1830).

Site in host: stomach.

Distribution: south-western WA.

Representative DNA sequence data: ITS1, 2: MF284678.

Diagnostic features (Fig. 5 D): Males: 4.3–6.0 mm; females 4.1–6.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule slightly wider than long, asymmetrical; anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending nearly to nerve ring; denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in posterior oesophageal region; bursal lobes of equal length; external branchlets of dorsal ray short; spicules 1.56–1.57 mm; spicule tip minutely bifid; spicule ala diminishes gradually to spicule tip, continued by flange surrounding tip; female tail conical; vagina long, straight; ovejector J-shaped.

***Cloacina chiron* Beveridge, 1999**

Cloacina chiron Beveridge, 1999b, pp. 24–25, figs 40–51.

Type data: holotype SAM AHC 30561, allotype SAM AHC 30562, paratypes SAM AHC 30563, BMNH 1998.9.28.5–6.

Type locality: Rottnest Island, WA (31° 59′S 115° 31′E).
Type host: *Setonix brachyurus* (Quoy & Gaimard, 1830).
Site in host: stomach.
Distribution: south-western WA.
Representative DNA sequence data: ITS1, 2: MF284679.
Diagnostic features (Figs 5 E, F): Males: 5.4–9.9 mm; females 8.5–12.3 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much larger than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule much wider than long, dorso-ventrally elongate, symmetrical; anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus with three lobes at anterior extremity, extending into base of buccal capsule; bosses, denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; dorsal lobe of bursa elongate; branchlets of dorsal ray short; spicules 0.58–0.65 mm; spicule tip bifid; spicule ala diminishes gradually to spicule tip, continued by flange surrounding tip; female tail conical; vagina short, straight; ovejector J-shaped.

***Cloacina circe* Beveridge, 1999**

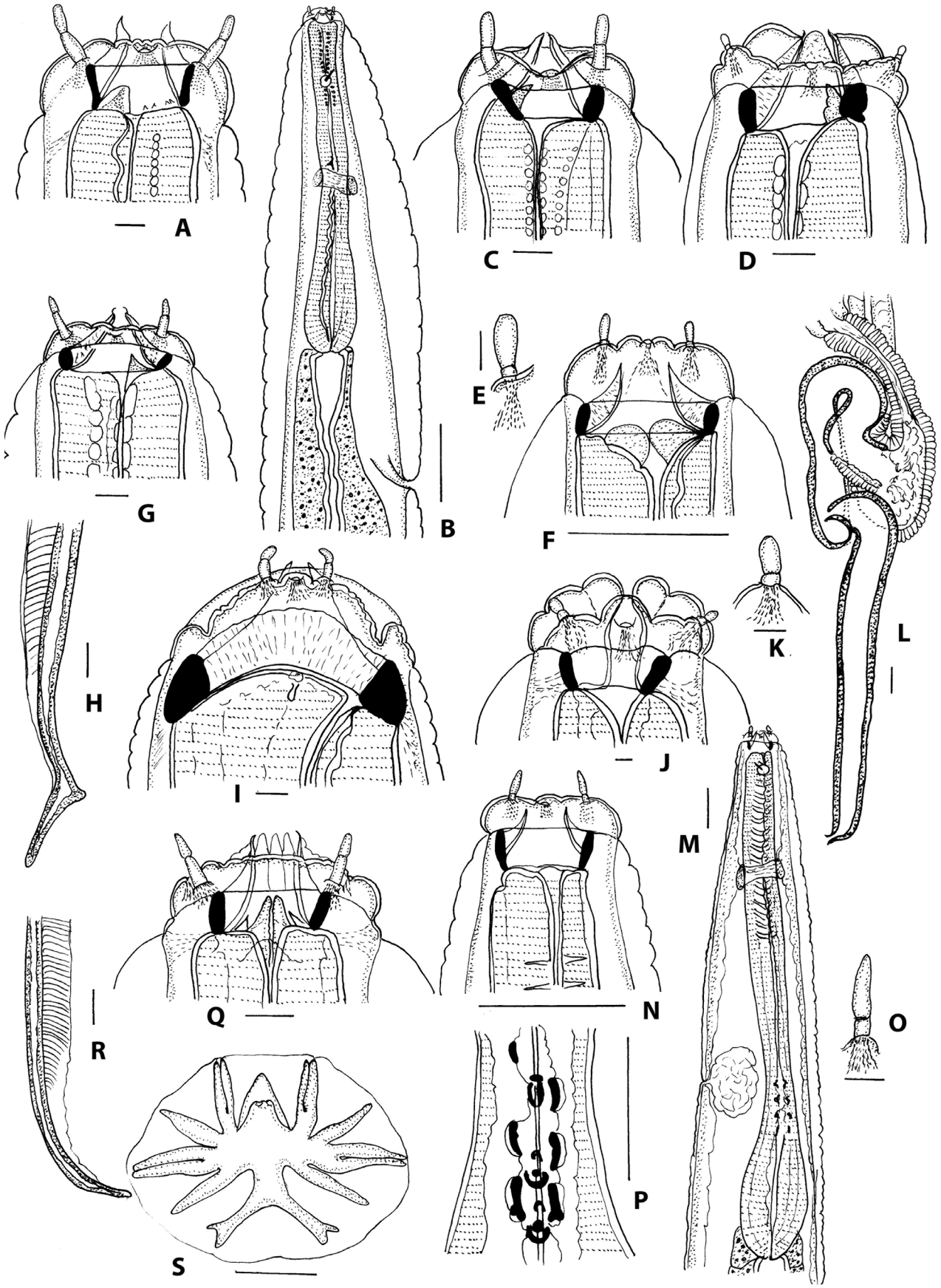
Cloacina circe Beveridge, 1999b, pp. 22–24, figs 29–39.
Type data: holotype SAM AHC 30564, allotype SAM AHC 30565, paratypes SAM AHC 30566, BMNH 1998.9.28.7–8.
Type locality: Rottnest Island, WA (31° 59′S 115° 31′E).
Type host: *Setonix brachyurus* (Quoy & Gaimard, 1830).
Site in host: stomach.
Distribution: south-western WA.
Representative DNA sequence data: ITS1, 2: MF284680.
Diagnostic features (Fig. 5 I): Males: 4.7–7.1 mm; females 7.3–10.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, oriented medially, much larger than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule much wider than long, dorso-ventrally elongate, symmetrical, arched anteriorly; bosses, denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in posterior oesophageal region; lobes of bursa of similar length; branchlets of dorsal ray short; spicules 0.97–1.35 mm; spicule tip blunt; spicule ala diminishes gradually to spicule tip; female tail conical; vagina short, straight; ovejector J-shaped.

***Cloacina cloelia* Beveridge, 1998**

Cloacina cloelia Beveridge, 1998a, pp. 315–317, figs 146–159; Griffith et al., 2000, p. 310.
Type data: holotype SAM AHC 26719, allotype SAM AHC 26720, paratypes SAM AHC 26721, BMNH 1996.3.19.16–17, USNPC 86365.
Type locality: Wongabel State Forest, Qld (17° 20′S 145° 29′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Other hosts: *Petrogale inornata* Gould, 1842; *Petrogale persephone* Maynes, 1982; *Thylogale calabyi* Flannery, 1992; *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: PNG, eastern Qld.
Diagnostic features (Figs 5 G, H): Males: 2.9–4.1 mm; females 3.2–4.9 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring; denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore in region of oesophago-intestinal junction; deirid in anterior oesophageal region; dorsal lobe of bursa elongate; branchlets of dorsal ray short; spicules 0.96–1.16 mm; spicule tip with characteristic hooked shape; spicule ala diminishes gradually to spicule tip; female tail conical; vagina short, straight; ovejector J-shaped.

Fig. 5. Genus *Cloacina*. A, *Cloacina castor*, buccal capsule, lateral view; B, *Cloacina celata*, anterior end, lateral view; C, *C. celata,* buccal capsule, lateral view; D, *Cloacina ceres*, buccal capsule, lateral view; E, *Cloacina chiron*, cephalic papilla; F, *C. chiron*, buccal capsule, lateral view; G, *Cloacina cloelia*, buccal capsule, lateral view; H, *C. cloelia*, spicule tip, lateral view; I, *Cloacina circe*, buccal capsule, lateral view; J, *Cloacina clymene*, buccal capsule, lateral view; K, *C. clymene*, cephalic papilla; L, *C. clymene*, vagina; M, *Cloacina communis*, anterior end, lateral view showing ornamentation of oesophagus; N, *C. communis*, buccal capsule, lateral view; O, *C. communis,* cephalic papilla; P, *C. communis*, oesophageal denticles, dorso-ventral view; Q, *Cloacina cornuta*, buccal capsule, dorsal view; R, *C. cornuta*, spicule tip, lateral view; S, *C. cornuta*, bursa, apical view. (A, G, H, M-S, from Beveridge, 1998a; B, C, from Beveridge, 2020f; D-F, I, from Beveridge, 1999b; J–L, from Beveridge et al., 2014b).

Scale-bars: B, F, L–N, P, S, 0.1 mm; A, C, D, E, G–K, O, Q, R, 0.01 mm.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Comments: *Cloacina cloelia* is readily identifiable by the characteristically hook–shaped spicule tips. It is primarily a parasite of *Thylogale* spp. but is also common in *Pet. persephone* (95% prevalence, Begg et al., 1996) which occurs in sympatry with *Thyl. stigmatica*. The record from *Pet. inornata* is a single collection (SAM AHC 15051) and was not included in Beveridge (1998a) but was included in Spratt & Beveridge (2016).

***Cloacina clymene* Beveridge, 1998**

Cloacina clymene Beveridge, 1998a, pp. 317–319, figs 160–172; Beveridge et al., 1998, p. 484; Beveridge et al., 2014b, pp. 3490–3491; Shuttleworth et al., 2016a, p. 247; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 26722, allotype SAM AHC 26723, paratypes SAM AHC 26724, 27378–80, BMNH 1996.3.19.18–19, USNPC 96366.

Type locality: 10 km NE of Warwick, Qld (28° 13′S 152° 02′E).

Type host: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: eastern Qld; NSW. Maps: Beveridge et al., 2014b, p. 3490; Beveridge, 2020c, p. 9.

Representative DNA sequence data: ITS1, 2: KM016822016824–5; KU853868, 853905.

Diagnostic features (Figs 5 J–L): Males 14.3–16.1 mm; females 18.0–25.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindical; distal segment ovoid, longer than proximal segment; lips prominent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin slightly undulating in lateral views, walls thickest anteriorly, directed antero-laterally; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 4.86–5.60 mm; spicule tip bifid; spicule ala diminishes gradually to spicule tip; female tail conical; distal vagina straight; anterior vagina recurrent; ovejector J-shaped.

Comments: *Cloacina clymene* is most similar to *C. atthis*. However, there are minor morphological differences as well as substantial differences in DNA sequence data. In addition, they are not closely related phylogenetically (Chilton et al., 2017). While *C. atthis* is limited to the Pilbara region of Western Australia, *C. clymene* occurs mainly along the east coast of Australia in the eastern wallaroo, *O. r. robustus*, with a single collection from the euro, *O. r. erubescens* in western New South Wales (Beveridge et al., 2014b).

***Cloacina communis* Johnston & Mawson, 1938**

Cloacina communis Johnston & Mawson, 1938, pp. 275–277, figs 38–41; 1939a, p. 133; 1940a, p. 468; 1940b, p. 97; Skrjabin et al., 1952, p. 160; Popova, 1960, pp. 12–13, fig. 3; Mawson, 1961a, p. 83; 1961b, p. 89; Yamaguti. 1961, p. 400; Arundel et al., 1979, p. 370; Chilton et al., 1997, p. 485; Beveridge et al., 1998, p. 484; Beveridge, 2016, p. 212; Shuttleworth et al., 2016a, p. 246; Beveridge, 2020c, p. 5.

Cloacina magna Johnston & Mawson, 1938, p. 227; Popova, 1960, pp. 28–29,

Type data: syntypes SAM V1355; paratypes, SAM AHC 1843.

Type locality: Mount Liebig, NT (23° 19′S 131° 22′E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Lagorchestes conspicillatus* Gould, 1842; *Notamacropus agilis* (Gould, 1842); *Notamacropus parryi* (Bennett, 1835); *Onychogalea unguifera* (Gould, 1840); *Osphranter antilopinus* (Gould, 1842); *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: NT, Qld, NSW, SA, WA. Maps: Chilton et al., 1997, p. 488; Shuttleworth et al., 2016a, p. 252.

Representative DNA sequence data: ITS1, 2: KU853876, 853890, 853892 853894–6, 853908, 853910–2, 853943–4, Y10795.

Diagnostic features (Figs 5 M–O, 44 C): Males 11.3–13.3 mm; females 16.0–35.0 mm; female tail distinctively coiled; cervical cuticle not inflated; cephalic papillae: proximal segment cylindical; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin straight in lateral views; oesophagus elongate without bosses; 3 triads of denticles immediately anterior to oesophageal bulb; 20–40 transverse folds in oesophageal corpus; nerve ring in anterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 3.62–4.90 mm; spicule ala diminishes gradually to spicule tip; female tail conical; vagina straight, very long; ovejector J–shaped.

Comments: This distinctive, large species is very common in *O. robustus* but also occurs in a variety of sympatric hosts at a lower prevalence (Beveridge et al., 1992, 1998). Genetic studies on this species using allozymes detected some differences between specimens from Port Augusta (South Australia) and Queensland (Chilton et al., 1997). Subsequent DNA sequence data revealed three clades, support-

ing the allozyme differences between Port Augusta and Queensland, but also identifying a third genetic group in eastern New South Wales, while associating the Queensland genotype with populations in the Northern Territory and Western Australia (Shuttleworth et al., 2016a, fig. 3 C). The genetics of this species warrant further investigation as there are obvious differences between geographically distinct populations.

The type material in SAM consists of two lots, the first (SAM V3155) containing 2 males and one female is labelled "syntypes", while the second (AHC 1843) is labelled "paratypes". All are from the same host and locality and there is no apparent reason for their current separate designations.

***Cloacina cornuta* (Davey & Wood, 1938)**

Macropostrongylus cornutus Davey & Wood, 1938, pp. 258–259, figs 1–2; Skrjabin et al., 1952, p.291; Popova, 1958, pp. 262–263, fig. 178; Yamaguti, 1961, p. 400.

Cloacina cornuta: Johnston & Mawson, 1939c, p. 208; Mawson, 1977c, p. 456, figs 1–4; Speare et al., 1983, p. 90; Beveridge et al., 1985, p. 378; Beveridge, 1998a, pp. 323–325, figs 187–198; Beveridge et al., 1998, p. 484; Beveridge, 2016, p. 212.

Type data: syntypes BMNH 1939.1.10.92–100, QM GL11300.

Type locality: Cromarty, Qld (19° 28'S 147° 03'E).

Type host: *Notamacropus agilis* (Gould, 1842).

Other hosts: *Thylogale brunii* (Schreber, 1778); *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: PNG, NT, Qld.

Representative DNA sequence data: ITS1, ITS2: MH105788–93.

Diagnostic features (Figs 5 Q–S): Males 6.2–9.2 mm; females 6.0–11.5 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindical; distal segment ovoid, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule slightly wider than long, dorsal wall directed anterolaterally; anterior margin straight in lateral views; dorsal oesophageal tooth projects into buccal capsule; oesophagus elongate without bosses; single dorsal denticle immediately anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 1.38–1.62 mm; spicule ala diminishes gradually to spicule tip; female tail swollen; vagina convoluted; ovejector J-shaped.

Comments: Specimens attributed to this species from *O. antilopinus* and *O. robustus* by Beveridge (1998a) have since been described as an independent species, *C. crassicaudata*. The record from *Wal. bicolor* was from a single collection since dessicated (Beveridge, 1998a); it requires confirmation.

***Cloacina crassicaudata* Beveridge, 2018**

Cloacina crassicaudata Beveridge, 2018 in Beveridge et al., 2018, pp. 534–538, figs 22–33; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 48104, allotype SAM AHC 48105, paratypes SAM AHC 48106.

Type locality: 46 km W of Victoria River, NT (15° 44'S 130° 45'E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Osphranter antilopinus* (Gould, 1842).

Site in host: stomach.

Distribution: WA, NT, Qld.

Representative DNA sequence data: ITS1, ITS2: MH105786 –7.

Diagnostic features (Figs 6 J–K): Males 5.5–7.2 mm; females 6.1–10.6 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical, slightly bulbous; distal segment ovoid, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, dorsal wall directed anterolaterally; anterior margin straight in lateral views; dorsal oesophageal tooth projects into buccal capsule; oesophagus elongate with bosses extending half way to nerve ring; single dorsal denticle immediately anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursal lobes of equal length; terminal branchlets of dorsal ray short; spicules 1.35–1.70 mm; spicule ala terminates anterior to spicule tip; female tail swollen; vagina convoluted; ovejector J-shaped.

Comments: This species has been included within *C. cornuta* in the past (Beveridge, 1998a).

***Cloacina cretheis* Beveridge, 2002**

Cloacina cretheis Beveridge, 2002b, pp. 2–5, figs 1–13.

Type data: holotype SAM AHC 31426, allotype SAM AHC 31427, paratypes SAM AHC 31428, BMNH 2001.4.10.1–2, USNPC 91133.

Type locality: Mount Somoro, Sandaun Province, PNG (3° 29'S 142° 02'E).

Type host: *Dendrolagus inustus* Müller, 1840.

Other hosts: *Dendrolagus dorianus* Ramsay; *Dendrolgus goodfellowi* Thomas; *Dendrolagus matschiei* Forster & Rothschild, 1907; *Dendrolagus scottae* Flannery & Seri-Tenkile, 1990.
Site in host: stomach.
Distribution: PNG.
Diagnostic features (Figs 6 A–C): Males: 6.9–9.0 mm; females 7.7–9.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical, slightly bulbous; distal segment ovoid, much shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule slightly wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in region of oesophago-intestinal junction; deirid in posterior oesophageal region; dorsal lobe of bursa elongate; external branchlets of dorsal ray arise anterior to principal bifurcation; internal branchlets diverge near extremity of dorsal ray; spicules 2.34–2.62 mm; spicule ala terminates abruptly anterior to spicule tip; female tail conical; vagina elongate, convoluted; ovejector J-shaped.
Comments: *Cloacina cretheis* occurs in a series of species of tree kangaroo in Papua New Guinea, but not in the Australian species of tree kangaroos.

***Cloacina cunctabunda* Beveridge, 2002**

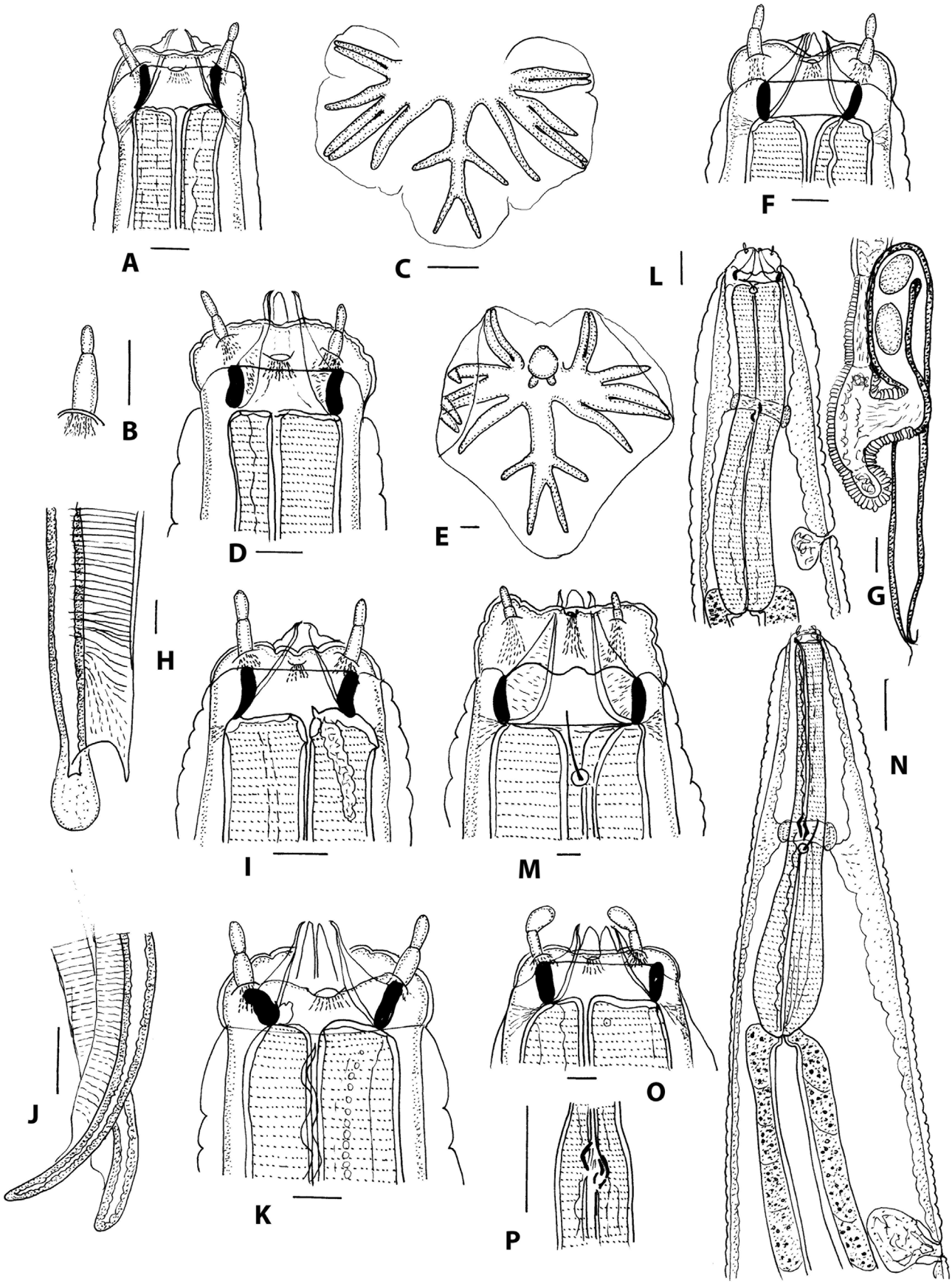
Cloacina cunctabunda Beveridge, 2002b, pp. 5–7, figs 14–23.
Type data: holotype SAM AHC 31432, allotype SAM AHC 31433, paratypes SAM AHC 28379.
Type locality: Camp Ridge, Tembagapura, Western New Guinea (4° 08′S 137° 05′E).
Type host: *Dendrolagus mbaiso* Flannery, Boeadi & Szalay, 1995.
Site in host: stomach.
Distribution: Western New Guinea.
Diagnostic features (Figs 6 D, E): Males: 3.30–3.32 mm; female 4.25 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical, slightly bulbous; distal segment ovoid, slightly longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa elongate; external branchlets of dorsal ray arise immediately anterior to principal bifurcation; internal branchlets diverge immediately after principal bifurcation; spicules 1.39–1.57 mm; female tail slender; vagina short with single convolution; ovejector J-shaped.
Comments: The description of this species is incomplete but is based on material collected from the holotype and only specimen of *Dend. mbaiso* in collections. Obtaining additional material is considered to be unlikely due to the rarity of the host.

***Cloacina curta* Johnston & Mawson, 1938**

Cloacina curta Johnston & Mawson, 1938, pp. 279–280, figs 51–54; Popova, 1960, pp. 13–15, fig. 4; Beveridge, 1998a, pp. 325–328, figs 199–211; 2020c, p. 4.
Type data: holotype and allotype SAM V1354, paratype SAM S1018.
Type locality: Mount Liebig, NT (23° 18′S 131° 22′E).
Type host: *Osphranter robustus* (Gould, 1840).
Other hosts: *Petrogale lateralis* Gould, 1840.
Site in host: stomach.
Distribution: WA (Kimberley Division), NT, Qld, SA.
Diagnostic features (Figs 6 F, G): Males: 5.4–9.2 mm; females 7.9–11.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, slightly shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa slightly longer than

Fig. 6. Genus *Cloacina*. A, *Cloacina cretheis*, buccal capsule, lateral view; B, *C. cretheis*, cephalic papilla; *C. cretheis*, bursa, apical view; D, *Cloacina cunctabunda*, buccal capsule, lateral view; E, *C. cunctabunda*, bursa, apical view; F, *Cloacina curta*, buccal capsule, lateral view; G, *C. curta*, vagina; H, *Cloacina cybele*, spicule tip, lateral view; I, *C. cybele*, buccal capsule, lateral view; J, *Cloacina crassicaudata*, spicule tips; K, *C. crassicaudata*, buccal capsule, lateral view; L, *Cloacina dahli*, anterior end, lateral view; M, *C. dahli*, buccal capsule, lateral view; N, *Cloacina daveyi*, anterior end, lateral view; O, *C. daveyi*, buccal capsule, lateral view; P, C. *daveyi*, oesophageal denticles. (A–C, from Beveridge, 2020f ; D, E, from Beveridge, 2002b; F–I, L–P, from Beveridge, 1998a; J, K, from Beveridge et al., 2018).

Scale-bars: C, E, G, L, N, P, 0.1 mm; A, B, D, F, H–K, M, O, 0.01 mm.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other lobes; terminal branchlets of dorsal ray variable in length; spicules 3.00–3.85 mm; female tail conical, short; distal vagina straight, proximal vagina recurrent; ovejector J-shaped.

Comments: Earlier reports of this species from *Mac. fuliginosus*, *N. irma*, *N. eugenii* and *Pet. xanthopus* in the literature cited by Beveridge (1998a) are not supported by extant specimens or confirmation from more recent collecting. They have been excluded from consideration here but may warrant future investigation. Beveridge (1998a) reported considerable morphological variation within this species which also warrants further study.

***Cloacina cybele* Beveridge, 1998**

Cloacina cybele Beveridge, 1998a, pp. 328–330, figs 212–233; Griffith et al., 2000, p. 310.

Type data: holotype SAM AHC 26725, allotype SAM AHC 26726, paratypes SAM AHC 26727, 27392–3, BMNH 1996.3.19.20–21, USNPC 86367.

Type locality: Mission Beach, Qld (17° 53′S 146° 06′E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Petrogale persephone* Maynes, 1982; *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: PNG, eastern Qld.

Diagnostic features (Figs 6 H, I): Males: 4.5–5.7 mm; females 4.5–6.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equivalent length; terminal branchlets of dorsal ray short; spicules 3.00–3.85 mm; ala terminating abruptly at spicule tip; spicule tip with prominent flange; female tail conical, short; distal vagina straight; ovejector J-shaped.

Comments: This species is readily distinguishable by the tips of the spicules.

***Cloacina dahli* von Linstow, 1898**

Cloacina dahli von Linstow, 1898, pp. 286–290, figs 13–20; Railliet & Henry, 1913, p. 507; Yorke & Maplestone, 1926, p. 176; Baylis & Daubney, 1926, p. 162; Skrjabin et al., 1952, p. 160; Popova, 1960, p. 10, fig. 1; Yamaguti, 1961, p. 399; Beveridge et al., 1989, p. 276; 1992, p. 364; Begg et al., 1995, p.47; Beveridge, 1998a, pp. 330–333, figs 224–237; Griffith et al., 2000, p. 310.

Type data: "syntypes" MNKB 3354; "paratypes" ZIMG 25409.

Type locality: Ralum, New Britain (4° 19′S 152° 14′E).

Type host: *Thylogale browni* (Ramsay, 1877).

Other hosts: *Petrogale persephone* Maynes, 1982; *Thylogale calabyi* Flannery, 1992; *Thylogale stigmatica* (Gould, 1860)

Site in host: stomach.

Distribution: PNG, eastern Qld.

Representative DNA sequence data: ITS1, ITS2: MF284681.

Diagnostic features (Figs 6 L, M, 44 D): Males 4.2–7.4 mm; females 6.7–9.9 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips present; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin undulate in lateral view; oesophagus sub-cylindrical without bosses; 3 denticles present at level of nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid immediately post-buccal; bursal lobes of equivalent length; terminal branchlets of dorsal ray short; spicules 2.00–2.35 mm; ala diminishing gradually to spicule tip; female tail conical, short, stout; distal vagina straight, with single loop at level of ovejector; ovejector J-shaped.

Comments: The only remaining specimens of this species in the Berlin Museum, were designated as "syntypes" by Beveridge (1998a). Other vials from the same collection had either been lost or the material had dessicated and there was no indication that any particular type specimens had been nominated. However, more recently, six specimens, clearly labelled as "paratypes" have been found in the Zoological Museum, University of Greifswold, Germany.

***Cloacina daveyi* Mawson, 1977**

Cloacina australis Johnston & Mawson, 1938, p. 275, figs 35–37; 1940b, p. 97; Skrjabin et al., 1952, p. 160; Popova, 1960, pp. 10, 12, fig. 2; Yamaguti, 1961, p. 399.

Cloacina daveyi Mawson, 1977b, p. 51, n.nom for *Cloacina australis* Johnston & Mawson, 1938; Beveridge & Arundel, 1979, p. 72; Beveridge, 1998a, pp. 333–335, figs 238–246; Shuttleworth et al., 2016a, p. 246; Beveridge, 2020c, p. 5.

Type data: holotype and allotype SAM V1358.

Type locality: Mount Liebig, NT (23° 18′S 131° 22′E).

Type host: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: WA, NT, NSW, SA. Maps: Shuttleworth et al., 2016a, p. 252; Beveridge, 2020c, p. 10.

Representative DNA sequence data: ITS1, ITS2: KY853840, 853909, 853941.

Diagnostic features (Figs 6 N–P): Males 5.4–9.8 mm; females 9.8–16.9 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment globose, directed medially, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; 3 denticles present at level of nerve ring; nerve ring in mid-oesophageal region; excretory pore markedly posterior to oesophago-intestinal junction; deirid at level of nerve ring; lobes of bursa of similar length; terminal branchlets of dorsal ray short; spicules 3.63–3.85 mm; female tail conical, short; distal vagina straight, proximal vagina recurrent; ovejector J-shaped.

Comments: While found moderately commonly in *O. robustus*, the published records from *Mac. fuliginosus* and *Mac. giganteus* cannot be confirmed in spite of relatively abundant collections of nematodes from these two species of kangaroos (Spratt & Beveridge, 2016) and the records have therefore been mentioned here, but they have not been included among the confirmed hosts.

Cloacina digitata Johnston & Mawson, 1940

Cloacina digitata Johnston & Mawson, 1940a, p. 469, figs 1–4; 1949, pp. 63, 66; Skrjabin et al., 1952, p. 160; Popova, 1960, p. 15, fig. 5; Yamaguti, 1961, p. 400; Beveridge, 1998a, pp. 335–338, figs 247–256.

Type data: syntypes SAM V1282, S1663.

Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Other hosts: *Petrogale herberti* Thomas, 1926; *Petrogale penicillata* (Gray, 1827).

Site in host: stomach.

Distribution: Qld.

Diagnostic features (Figs 7 A, B): Males: 7.2–8.7 mm; females 9.2–13.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in anterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursal lobes of equivalent length; terminal branchlets of dorsal ray short; spicules 2.50–2.80 mm; ala diminishing gradually to spicule tip; female tail conical, short; distal vagina straight, proximal vagina convoluted and recurrent at entry to ovejector; ovejector J-shaped.

Comments: The identity of this species is uncertain. Johnston & Mawson (1940a) described this species from *N. dorsalis* and subsequently added records from *N. agilis* (Johnston & Mawson, 1949). However, current extensive collections from both of these host species have not confirmed the original records, while nematodes fitting the original description have been found in *Pet. herberti* and *Pet. penicillata* (Beveridge, 1998a), an inconsistency which awaits resolution.

Cloacina dindymene Beveridge, 1998

Cloacina dindymene Beveridge, 1998a, pp. 338–340, figs 257–264; Beveridge et al., 1998, p. 484; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 26731, allotype SAM AHC 26732, paratypes SAM AHC 26733–5, 27402–6.

Type locality: Harvest Home Station via Charters Towers, Qld (20° 42′S 146° 38′E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Osphranter antilopinus* (Gould, 1842).

Site in host: stomach.

Distribution: WA (Kimberley Division), NT, Qld. Map: Beveridge, 2020c, p. 8.

Representative DNA sequence data: ITS1, ITS2: MF284682.

Diagnostic features (Fig. 7 C): Males: 5.0–6.2 mm; females 5.8–6.9 mm; cervical cuticle inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, slender, longer than proximal segment; lips present; 8 leaf-crown elements; buccal capsule slightly wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; single dorsal denticle present immediately anterior to nerve ring; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursal lobes of equivalent length; terminal branchlets of dorsal ray short; spicules 2.40–2.67 mm; female tail conical; distal vagina straight, recurrent at entry to ovejector; ovejector J-shaped.

Cloacina dirce Beveridge, 1998

Cloacina dirce Beveridge, 1998a, pp. 340–342, figs 265–276; Beveridge et al., 1998, p. 484; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 26728, allotype SAM AHC

26729, paratypes SAM AHC 26730, 27407–9, BMNH 1996.3.20.3–4, USNPC 86396.

Type locality: 20 km E of Mount Surprise, Qld (18° 16′S 143° 29′E).

Type host: *Osphranter antilopinus* (Gould, 1842).

Other hosts: *Ospharanter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: WA (Kimberley Division), NT, Qld.

Representative DNA sequence data: ITS1, ITS2: MF284683.

Diagnostic features (Figs 7 D–F): Males: 6.3–7.2 mm; females 7.8–8.6 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, slender, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule slightly wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; single dorsal denticle present immediately anterior to nerve ring; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equivalent length; terminal branchlets of dorsal ray short; spicules 3.48–3.95 mm; female tail conical; vagina highly convoluted; ovejector J-shaped.

***Cloacina dis* Beveridge, 1998**

Cloacina dis Beveridge, 1998a, pp. 342–344, figs 277–289; Beveridge et al., 1998, p. 484; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 26736, allotype SAM AHC 26737, paratypes SAM AHC 26739–42, BMNH 1996.3.20.5–6, USNPC 86370.

Type locality: Harvest Home Station via Charters Towers, Qld (20° 42′S 146° 38′E).

Type host: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: north-eastern Qld. Map: Beveridge, 2020c, p. 11.

Diagnostic features (Figs 7 G–I): Males: 7.0–10.0 mm; females 6.4–10.3 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment conical, slender, much shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, shallow, asymmetrical with ventral wall longer than dorsal wall, anterior margin straight to slightly arched in lateral view; oesophagus with bosses extending almost to nerve ring; single dorsal denticle present immediately anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursal lobes of equivalent length; terminal branchlets of dorsal ray short; spicules 4.45–5.30 mm; female tail conical, stout; vagina highly convoluted arranged spirally in mid-region; ovejector J-shaped.

Comments: Although readily distinguishable by the spirally coiled vagina in the female, the gubernaculum of this species is particularly prominent and the junction of the spicule sheaths is surrounded by prominent musculature.

***Cloacina dryope* Beveridge, 1998**

Cloacina dryope Beveridge, 1998a, pp. 344–346, figs 290–301; Beveridge et al., 1998, p. 483.

Type data: holotype SAM AHC 26828, allotype SAM AHC 26829.

Type locality: Rockhampton, Qld (23° 22′S 150° 32′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

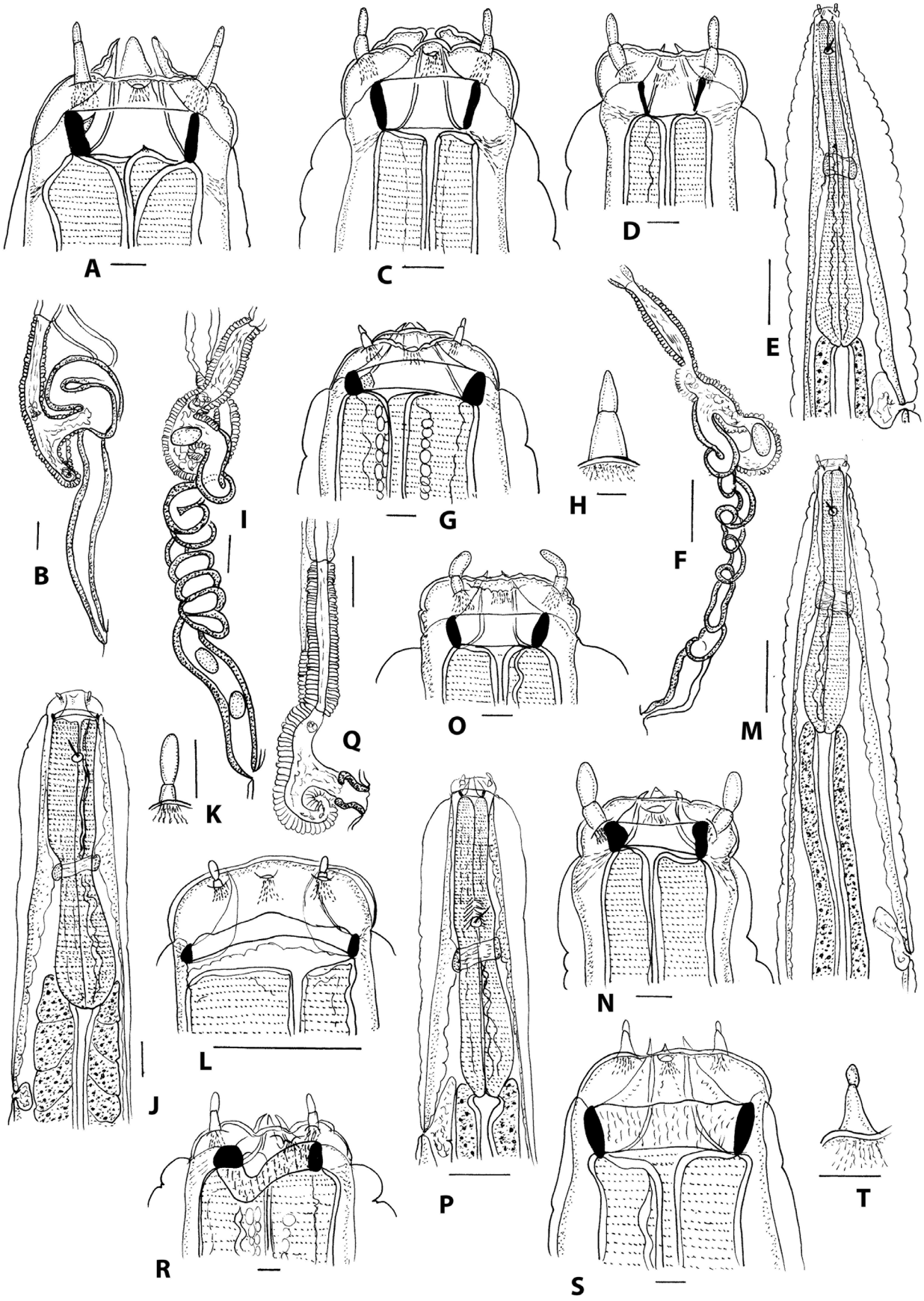
Distribution: eastern Qld.

Representative DNA sequence data: ITS1, ITS2: MF284684.

Diagnostic features (Figs 7 J–L): Males 5.1–6.6 mm; females 5.3–7.5 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; mouth opening dorso-ventrally elongate; buccal capsule much wider than long, very shallow, symmetrical, anteriorly arcuate in lateral view, arcuate posteriorly in dorsal and ventral views; oesophagus constricted at level of nerve ring, without bosses, denticles and

Fig. 7. Genus *Cloacina*. A, *Cloacina digitata*, buccal capsule, lateral view; B, *C. digitata*, vagina; C, *Cloacina dindymene*, buccal capsule, lateral view; D, *Cloacina dirce*, buccal capsule, lateral view; E, *C. dirce*, anterior end, lateral view; F, *C. dirce*, vagina; G, *Cloacina dis*, buccal capsule, lateral view; H, *C. dis*, cephalic papilla; I, *C. dis*, vagina; J, *Cloacina dryope*, anterior end, lateral view; K, *C. dryope*, cephalic papilla; L, *C. dryope*, buccal capsule, lateral view; M, *Cloacina echidne*, anterior end, lateral view; N, *C. echidne*, buccal capsule, lateral view; O, *Cloacina edwardsi*, buccal capsule, lateral view; P, *C. edwardsi*, anterior end, lateral view; Q, *C. edwardsi*, vagina; R, *Cloacina eileithyia*, buccal capsule, lateral view; S, *Cloacina elegans*, buccal capsule, lateral view; T, *C. elegans*, cephalic papilla. (A–R, from Beveridge, 1998a; S, T, from Beveridge, 2019).

Scale-bars: B, E, F, I, J, L, M, P, Q, 0.1 mm; A, C, D, G, H, K, N, O, R–T, 0.01 mm.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folds; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equivalent length; spicules 1.75–2.03 mm; female tail conical; vagina straight; ovejector J-shaped.

Cloacina dubia* Johnston & Mawson, 1938 *species inquirenda

Cloacina dubia Johnston & Mawson, 1938, pp. 280–281, figs 55–57; Skrjabin et al., 1952, p. 160; Popova, 1960, p. 16, fig. 6; Yamaguti, 1961, p. 400; Beveridge, 1998a, p. 501.

Type data: holotype and allotype SAM V1357.

Type locality: Mount Liebig, NT (23° 18′S 131° 22′E).

Type host: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Comments: The type specimens were re–examined by Beveridge (1998a) but both lack all four cephalic papillae rendering their identification impossible. The species was therefore designated as *inquirenda*.

***Cloacina echidne* Beveridge, 1998**

Cloacina echidne Beveridge, 1998a, pp. 346–349, figs 302–312; Beveridge et al., 1989, p. 484; Bradley et al., 2000, p. 39; Shuttleworth et al., 2016a, p. 247; Beveridge, 2016, p. 213; 2020c, p. 5.

Type data: holotype SAM AHC 26810, allotype SAM AHC 26811, paratypes SAM AHC 26812, 27415.

Type locality: Fletcher View Station via Charters Towers, Qld (19° 53′S 146°10′E).

Type host: *Lagorchestes conspicillatus* Gould, 1842.

Other hosts: *Osphranter antilopinus* (Gould, 1842); *Osphranter robustus* (Gould, 1840); *Petrogale purpureicollis* Le Souef, 1924; *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: WA (Kimberley Division), Qld, SA.

Representative DNA sequence data: ITS1, ITS2: KU853841, 853856, 853924.

Diagnostic features (Figs 7 M, N): Males 7.3–7.5 mm; females 7.3–9.2 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore well posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equivalent length; spicules 1.22–1.50 mm; female tail slender; vagina straight; ovejector J-shaped.

Comments: Current data suggest that *C. echidne* is primarily a parasite of *O. robustus* (Beveridge, 2020c), with *La. conspicillatus* and *Wal. bicolor* representing incidental hosts. The significance of *O. antilopinus* as a host remains to be determined.

***Cloacina edwardsi* Mawson, 1972**

Cloacina edwardsi Mawson, 1972, p. 112, figs 14–22; Beveridge, 1979, p. 364; Beveridge et al., 1985, p. 378; Beveridge, 1998a, pp. 349–351, figs 313–323; Beveridge et al., 1998, p. 485; Aussavy et al., 2011, p. 17; Shuttleworth et al., 2014, p. 263; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 213; Spratt et al., 2017, p. 242.

Type data: holotype and allotype, SAM V1507.

Type locality: Sunday Island, Vic (38° 43′S 136° 48′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: Qld, NSW, Vic.

Representative DNA sequence data: ITS1, ITS2: KM219842–5, 219919–22; 18S, 28S, ITS: MF284685.

Diagnostic features (Figs 7 O–Q): Males 5.0–7.4 mm; females 6.9–8.9 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment doliiform, longer than proximal segment, directed medially; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus without bosses and folds; plumose thickening of oesophageal lining immediately anterior to nerve ring; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equivalent length; external branchlets of dorsal ray short; spicules 0.41–0.47 mm; ala terminates abruptly immediately anterior to spicule tip; female tail slender; vagina straight; ovejector J-shaped.

Comments: This highly characteristic species is a common parasite of *Wal. bicolor* throughout its geographical range (Beveridge, 2016). Shuttleworth et al. (2014) found little genetic variation within this species throughout its geographical range.

***Cloacina eileithyia* Beveridge, 1998**

Cloacina eileithyia Beveridge, 1998a, pp. 351–353, figs 324–338; 2020c, p. 5.

Type data: holotype SAM AHC 27335, allotype SAM AHC 27336, paratypes SAM AHC 27337, 27418–20, BMNH 1996.3.20.9–19, USNPC 86372.

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Osphranter antilopinus* (Gould, 1842).

Site in host: stomach.
Distribution: WA (Kimberley Division), NT, Qld.
Diagnostic features (Fig. 7 R): Males: 5.8–8.1 mm; females 8.5–10.8 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, slender, as long as proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, shallow, asymmetrical with dorsal wall more robust than ventral wall, buccal capsule sinuous in lateral view, arched in dorsal and ventral views; oesophagus with bosses extending almost to nerve ring; single dorsal denticle present immediately anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursal lobes of equivalent length; terminal branchlets of dorsal ray short; spicules 2.30–2.40 mm; ala terminates anterior to spicule tip, continuing as flange around tip; female tail slender; vagina straight; ovejector J-shaped.
Comments: The species is immediately recognisable based on the shape of the buccal capsule in lateral view.

***Cloacina elegans* Johnston & Mawson, 1938**

Cloacina elegans Johnston & Mawson, 1938, pp. 271–273; figs 23–27; Skrjabin et al., 1952, p. 160; Popova, 1960, pp. 16 –18, fig. 7; Yamaguti, 1961, p. 400; Beveridge, 1998a, pp. 353–355, figs 339–345; 2019, pp. 2–6, figs 1–10.
Type data: syntypes SAM V1427.
Type locality: Hermannsburg, NT (23° 57′S 132° 46′E).
Type host: *Petrogale lateralis* Gould, 1840 (MacDonnell Ranges race).
Site in host: stomach.
Distribution: NT (Central Australia).
Diagnostic features (Figs 7 S, T): Males 4.8–7.3 mm; females 8.6–10.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment tapering; distal segment ovoid, much shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes of equivalent length; branchlets of dorsal ray short; spicules 1.93–2.15 mm; spicule tip recurved; ala diminishes in width to tip; female tail conical; vagina short, prominently recurrent; ovejector J-shaped.
Comments: Beveridge (1998a) redescribed this species from the type specimens, which were in a very poor state of preservation. The only material which has come to hand since is a single collection, including a single male, from the type host and close to the type locality. The description of the new material (Beveridge, 2019) remains limited particularly with respect to metric data for the male.

***Cloacina enyo* Beveridge, 1998**

Cloacina enyo Beveridge, 1998a, pp. 355–357, figs 346–354.
Type data: holotype and allotype SAM AHC 26749, paratypes SAM AHC 10811, 27424–5.
Type locality: Mount Borradaile, NT (12° 03′S 132°54′E).
Type host: *Petrogale wilkinsi* Thomas, 1926 (as *Petrogale brachyotis* (Gould, 1841)).
Site in host: stomach.
Distribution: NT (Top End).
Diagnostic features (Figs 8 A, B): Males: 2.4–2.8 mm; females 2.7–3.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; dorsal lobe of bursa of elongate; external branchlets of dorsal ray short, arise anterior to principal bifurcation; spicules 0.68–0.88 mm; female tail conical; vagina straight; ovejector J-shaped.
Comments: Although originally described from "*Petrogale brachyotis*", the host of the type specimens has recently been determined to be *Pet. wilkinsi*.

***Cloacina eos* Beveridge, 1998**

Cloacina eos Beveridge, 1998a, pp. 357–359, figs 355–367; Beveridge et al., 1998, p. 485; Aussavy et al., 2011, p. 17; Shuttleworth et al., 2014, p. 263; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 213; Spratt et al., 2017, p. 242.
Type data: holotype SAM AHC 26825, allotype SAM AHC 26826, paratypes SAM AHC 26827, BMNH 1996.3.20.12–13, USNPC 86374.
Type locality: O'Hara's Hill, Proserpine, Qld (20° 24′S 148° 36′E).
Type host: *Wallabia bicolor* (Desmarest, 1804).
Site in host: stomach.
Distribution: Qld, NSW, Vic.

Representative DNA sequence data: ITS1, ITS2: KM219912–18, 2198452.

Diagnostic features (Figs 8 C–E): Males: 5.9–7.1 mm; females 7.2–8.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, slender, much shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending almost to nerve ring, denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in posterior oesophageal region; bursal lobes of equivalent length; terminal branchlets of dorsal ray short; spicules 2.40–2.67 mm; ala diminishes gradually to tip; female tail conical; distal vagina straight, proximal vagina recurrent; ovejector J-shaped.

Comments: This species was included within *C. papillata* by Beveridge (1979) but was recognised as a distinct species by Beveridge (1998a). Genetic studies by Shuttleworth et al. (2014) and Chilton et al. (2017) have shown that these are sister species, but their genetic rather than the morphological separation was not always clear in the data presented by Shuttleworth et al. (2014). This species pair therefore warrants more intensive molecular examination.

***Cloacina epona* Beveridge, 1998**

Cloacina epona Beveridge, 1998a, pp. 359–362, figs 368–377; Shuttleworth et al., 2016c, p. 246; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 26743, allotype SAM AHC 26744, paratypes SAM AHC 26745–8, 27426–9, BMNH 1996.3.20.14–15, USNPC 86375.

Type locality: Oban Station via Mount Isa, Qld (21° 14′S 139° 03′E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Lagorchestes hirsutus* Gould, 1844 (captive).

Site in host: stomach.

Distribution: NT, Qld. Maps: Shuttleworth et al., 2016a, p. 252; Beveridge, 2020, p. 10.

Representative DNA sequence data: ITS1, ITS2: KU853844, 853854, 853914.

Diagnostic features (Figs 8 F–H): Males 6.3–10.4 mm; females 8.7–16.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment globose, directed medially, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin slightly sinuous in lateral view; oesophagus without bosses and folds; 3 sets of denticles present posterior to nerve ring; nerve ring in anterior oesophageal region; excretory in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa of similar length; terminal branchlets of dorsal ray short; spicules 0.96–1.15 mm; female tail conical, short; vagina straight, short; ovejector J-shaped.

***Cloacina erigone* Beveridge, 2002**

Cloacina erigone Beveridge, 2002b, pp. 7–9, figs 24–36; Spratt & Beveridge, 2016, p. 127.

Type data: holotype SAM AHC 31434, allotype SAM AHC 31435, paratypes SAM AHC 31436, BMNH 2001.4.10.3–4, USNPC 91134.

Type locality: Usino, Madang, PNG (5° 32′S 145° 23′E).

Type host: *Dorcopsis hageni* Heller, 1897.

Other hosts: *Dorcopsis muelleri* (Schlegel, 1866).

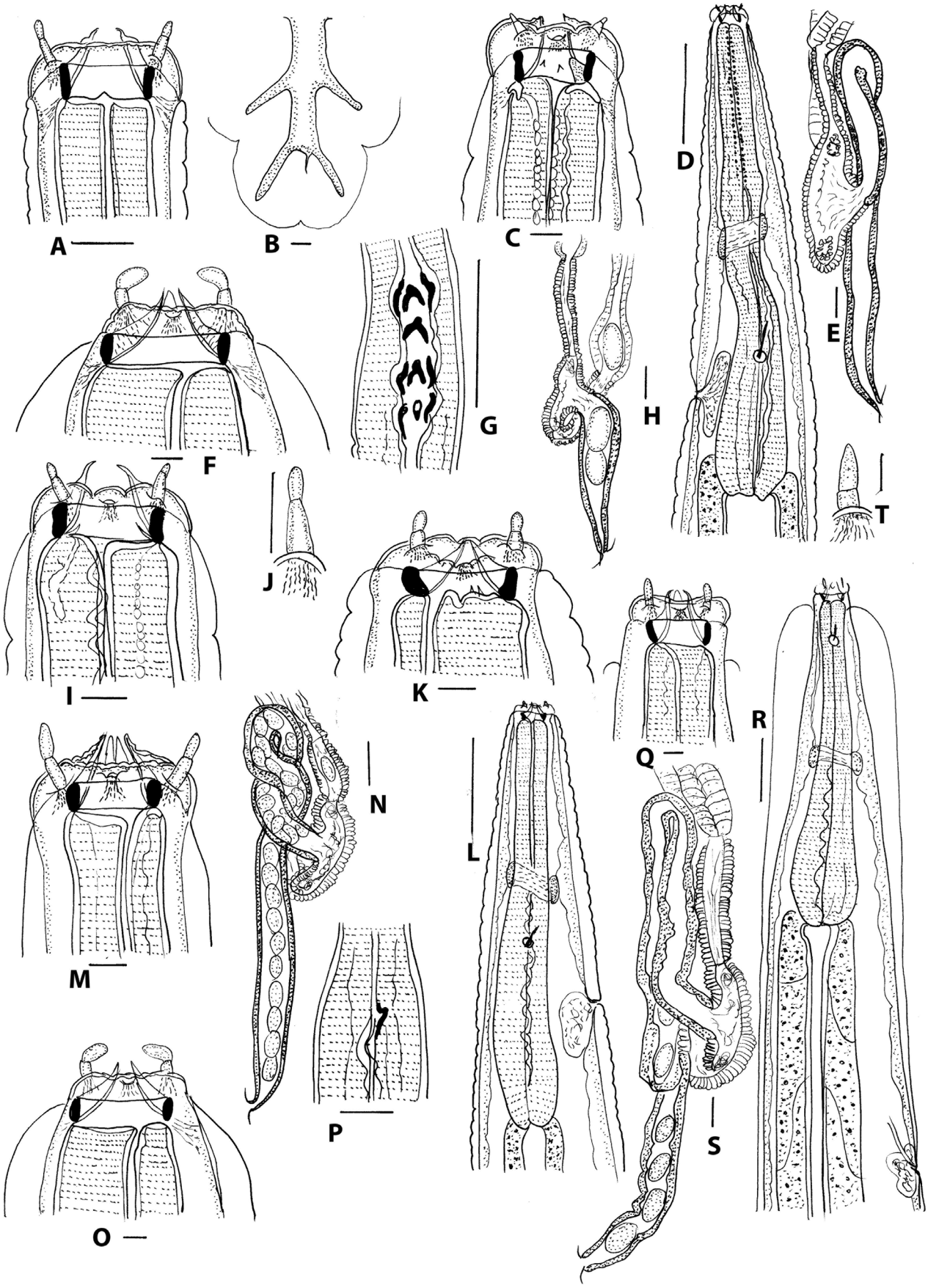
Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 8 I–J): Males: 2.90–5.61 mm; females 3.60–4.58 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral view; oesophagus with bosses extending halfway to nerve ring; single denticle anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junc-

Fig. 8. Genus *Cloacina*. A. *Cloacina enyo*, buccal capsule, dorsal view; B. *C. enyo*, dorsal ray of bursa; C, *Cloacina eos*, buccal capsule, lateral view; D, *C. eos*, anterior end, lateral view; E, *C. eos*, vagina and ovejector; F, *Cloacina epona*, buccal capsule, lateral view; G, *C. epona*, oesophageal denticles, dorso-ventral view; H, *C. epona*, vagina and ovejector, lateral view; I, *Cloacina erigone*, buccal capsule, lateral view; J, *C. erigone*, cephalic papilla; K, *Cloacina eris*, buccal capsule, lateral view; L, *C. eris*, anterior end, lateral view; M, *Cloacina eurynome*, buccal capsule, lateral view; N, *C. eurynome*, vagina and ovejector, lateral view; O, *Cloacina ernabella*, buccal capsule, lateral view; P, *C. ernabella*, oesophageal denticle; Q, *Cloacina expansa*, buccal capsule, lateral view; R, *C. expansa*, anterior end, lateral view; S, *C. expansa*, vagina and ovejector, lateral view; T, *C. expansa*, cephalic papilla. (A–T, from Beveridge, 1998a).

Scale-bars: D, E, H, L, N, R, S, 0.1 mm; A–C, F, G, I–K, M, O, P, Q, T. 0.01 mm.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tion; deirid in posterior oesophageal region; dorsal lobe of bursa of elongate; external branchlets of dorsal ray short immediately anterior to principal bifurcation; spicules 1.35–1.79 mm; female tail conical; vagina straight; ovejector Jshaped.

Comments: Beveridge (2002b) reported the species from *Dorcopsis hageni*; an additional host species, *Dc. muelleri*, was added by Spratt & Beveridge (2016).

***Cloacina eris* Beveridge, 2018**

Cloacina eris Beveridge, 2018, pp. 200–204, figs 11–21; 2020e, p. 204.

Type data: holotype SAM AHC 48185, allotype SAM AHC 48186, paratypes SAM AHC 48187.

Type locality: Etna Station via Kynuna, Qld (21° 42′S 142° 15′E).

Type host: *Osphranter rufus* (Desmarest, 1822).

Site in host: stomach.

Distribution: Qld, WA. Map: Beveridge, 2018, p. 205.

Diagnostic features (Figs 8 K, L): Males: 11.4–12.8 mm; females 13.5–16.2 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, much shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical; anterior margin straight in lateral views; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid posterior to nerve ring; bursal lobes of equal length; external branchlets of dorsal ray arising immediately after principal bifurcation; spicules 2.11–2.44 mm; spicule ala diminishes in width to spicule tip; female tail conical; vagina convoluted; ovejector J-shaped.

Comments: This species is most similar to *C. ares*. See comments under that species.

***Cloacina ernabella* Johnston & Mawson, 1938**

Cloacina ernabella Johnston & Mawson, 1938, pp. 281–282, figs 58–62; Skrjabin et al., 1952, p. 160, fig. 78; Popova, 1960, pp. 18–19, fig. 8; Yamaguti, 1961, p. 400; Beveridge et al., 1989, p. 276; Beveridge, 1998a, pp. 362–364, figs 378–388; Bradley et al., 2000, p. 39.

Type data: holotype and allotype SAM V1351.

Type locality: Ernabella, SA (26° 17′S 132° 08′E).

Type host: *Petrogale lateralis* Gould,1840 (MacDonnell Ranges race).

Other hosts: *Petrogale purpureicollis* Le Souef, 1924.

Site in host: stomach.

Distribution: Qld, SA.

Representative DNA sequence data: ITS1, ITS2: FM992596–8; cox1: KJ851926; 18S, 28S, ITS KJ776346.

Diagnostic features (Figs 8 O, P): Males 5.5–7.9 mm; females 5.6–8.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment globose, directed medially, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; single dorsal denticle present posterior to nerve ring; nerve ring in anterior oesophageal region; excretory pore posterior to oesophagointestinal junction; deirid in anterior oesophageal region; lobes of bursa of similar length; terminal branchlets of dorsal ray short; spicules 1.42–1.85 mm; ala diminishes gradually towards tip; female tail conical, short; vagina straight, short; ovejector J-shaped.

Comments: Current collections suggest a disjunct distribution for this species with the type specimens described from *Pet. lateralis* in South Australia and with more recent collections from *Pet. purpureicollis* (formerly a sub-species of *Pet. lateralis*) in Queensland, but with no collections from *Pet. lateralis* in the Northern Territory, between these two known localities. Chilton et al. (2009) demonstrated significant genetic differences between specimens of *C. ernabella* from Cloncurry and Mary Kathleen compared with those from an isolated population near Winton, Queensland. Consequently, molecular data from the Ernabella population in South Australia would be of interest in determining the genetic relationships within this species.

***Cloacina eurynome* Beveridge, 2002**

Cloacina eurynome Beveridge, 2002b, pp. 9–11, figs 37–49.

Type data: holotype SAM AHC 31437, allotype SAM AHC 31438, paratypes SAM AHC 31439–40, BMNH 2001.4.10.5–6, USNPC 91135.

Type locality: Tembagapura, Western New Guinea (4° 08′S 137° 05′E).

Type host: *Dendrolagus dorianus* Ramsay, 1883.

Other hosts: *Dendrolagus scottae* Flannery & Seri–Tenkile.

Site in host: stomach.

Distribution: PNG, Western New Guinea.

Diagnostic features (Figs 8 M, N): Males: 8.8–10.7 mm; females 10.1–13.3 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in

lateral view; oesophagus without bosses and folds; single dorsal denticle anterior to nerve ring; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid at level of nerve ring; lobes of bursa of similar size; external branchlets of dorsal ray arise after principal bifurcation; spicules 3.57–3.98 mm; ala terminates abruptly anterior to tip, continued by flange around tip; female tail conical; distal vagina straight; proximal vagina recurrent, coiled around ascending vagina; ovejector J-shaped.

Comment: A unique feature of this species is the intercoiling of the ascending and recurrent descending arms of the vagina.

***Cloacina expansa* Johnston & Mawson, 1939**

Cloacina expansa Johnston & Mawson, 1939b, p. 529, figs 42–45; Skrjabin et al., 1952, p. 160; Popova, 1960, p.19, fig. 9; Yamaguti, 1961, p. 400; Beveridge & Arundel, 1979, pp. 72, 74; Arundel et al., 1990, p. 42; Pamment et al., 1994, p. 193; Beveridge, 1998a, pp. 364–366, figs 389–398; Beveridge et al., 1998, p. 485; Aussavy et al., 2011, pp. 14, 15; Schultz et al., 2011, p. 238; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p.168; Spratt et al., 2017 p. 240.

Type data: syntypes SAM V1564.

Type locality: Coonamble, NSW (30° 57′S 128° 34′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817); *Petrogale penicillata* (Gray, 1827).

Site in host: stomach.

Distribution: Qld, NSW, Vic, SA, WA.

Diagnostic features (Figs 8 Q–T, 44 E): Males: 10.0–11.6 mm; females 11.1–16.1 mm; cervical cuticle very prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight in lateral view; oesophagus without bosses denticles and folds; nerve ring in mid-oesophageal region; excretory pore well posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa of similar size; branchlets of dorsal ray short; spicules 5.0–6.5 mm; ala diminishes gradually to tip; female tail conical, short; distal vagina straight; proximal vagina recurrent; ovejector J-shaped.

Comments: *Cloacina expansa* is a common parasite of both eastern and western grey kangaroos, *Mac. giganteus* and *Mac. fuliginosus* (Beveridge & Arundel, 1979). The single record from *Pet. penicillata* (Schultz et al., 2011) is from a captive–bred animal released into a zone of sympatry with both grey kangaroo species.

***Cloacina feronia* Beveridge, 1998**

Cloacina feronia Beveridge, 1998a, pp. 366–369, figs 399–410; Beveridge et al., 1989, p. 485; Shuttleworth et al., 2016a, pp. 246, 252; Beveridge 2020c, p. 5.

Type data: holotype SAM AHC 26752, allotype SAM AHC 26753, paratypes SAM AHC 26754, 27436–8.

Type locality: Spear Creek Station via Port Augusta, SA (32° 34′S 137° 59′E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Macropus giganteus* Shaw, 1790; *Notamacropus dorsalis* (Gray, 1837); *Petrogale assimilis* Ramsay, 1877; *Petrogale xanthopus* Gray, 1855.

Site in host: stomach.

Distribution: WA, NT, Qld, NSW, SA. Map: Shuttleworth et al., 2016, p. 252.

Representative DNA sequence data: ITS1, ITS2: KU 853848–50, 853855, 853864, 853869, 853878, 853893, 853916–7, 853942, 853951.

Diagnostic features (Figs 9 A, B): Males 10.1–11.4 mm; females 13.5–19.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment globose, directed medially, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin sinuous in lateral view; oesophagus without bosses and folds; 5 groups of 3 denticles present posterior to nerve ring; nerve ring in anterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa of similar length; terminal branchlets of dorsal ray short; spicules 1.65–1.85 mm; female tail conical, short; vagina straight, short; ovejector J-shaped.

Comments: Collection data to date suggest that the principal host of *C. feronia* is *O. robustus*, with *Mac. giganteus*, *N. dorsalis*, *Pet. assimilis* and *Pet. xanthopus* being uncommon hosts in areas where they are sympatric with *O. robustus*.

***Cloacina frequens* Johnston & Mawson, 1938**

Cloacina frequens Johnston & Mawson, 1938, pp. 273–274, figs 32–34; Skrjabin et al., 1952, p. 161; Popova, 1960, pp. 20–21, fig. 10; Yamaguti, 1961, p. 400; Beveridge, 1998a, pp. 369–371, figs 411–421; Beveridge et al, 1998, p. 485; Bradley et al., 2000, p. 39; Shuttleworth et al., 2016a, pp. 246, 252; Beveridge 2020c, p. 5.

Type data: holotype and allotype SAM V1359, paratype SAM AHC 21686.
Type locality: Mount Liebig, NT (23° 19'S 131° 22'E).
Type host: *Osphranter robustus* (Gould, 1840).
Other hosts: *O. antilopinus* (Gould, 1842); *Petrogale purpureicollis* Le Souef, 1924.
Site in host: stomach.
Distribution: NT, Qld. Map: Shuttleworth et al., 2016a, p. 252.
Representative DNA sequence data: ITS1, ITS2: KU853830, 853891, 853906–7.
Diagnostic features (Fig. 9 C, 44 F): Males 9.1–12.3 mm; females 17.7–23.8 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment globose, directed medially, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin slightly sinuous in lateral view; oesophagus without bosses and folds; 5 groups of 3 denticles present posterior to nerve ring; nerve ring in anterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa of similar length; terminal branchlets of dorsal ray short; spicules 1.02–1.10 mm; female tail conical, short; vagina straight, short; ovejector Y-shaped.
Comments: Most of the current records of this species are from *O. robustus*, with fewer reports from the sympatric host species *O. antilopinus* and *Pet. purpureicollis*. Reports from *Mac. giganteus* and *Pet. xanthopus* by Johnston & Mawson (1940b) are unconfirmed and have not been included. They may have been *C. feronia* which is a similar species which had not been identified at that time.

Cloacina galatea Beveridge, Jabbar & Shuttleworth, 2014

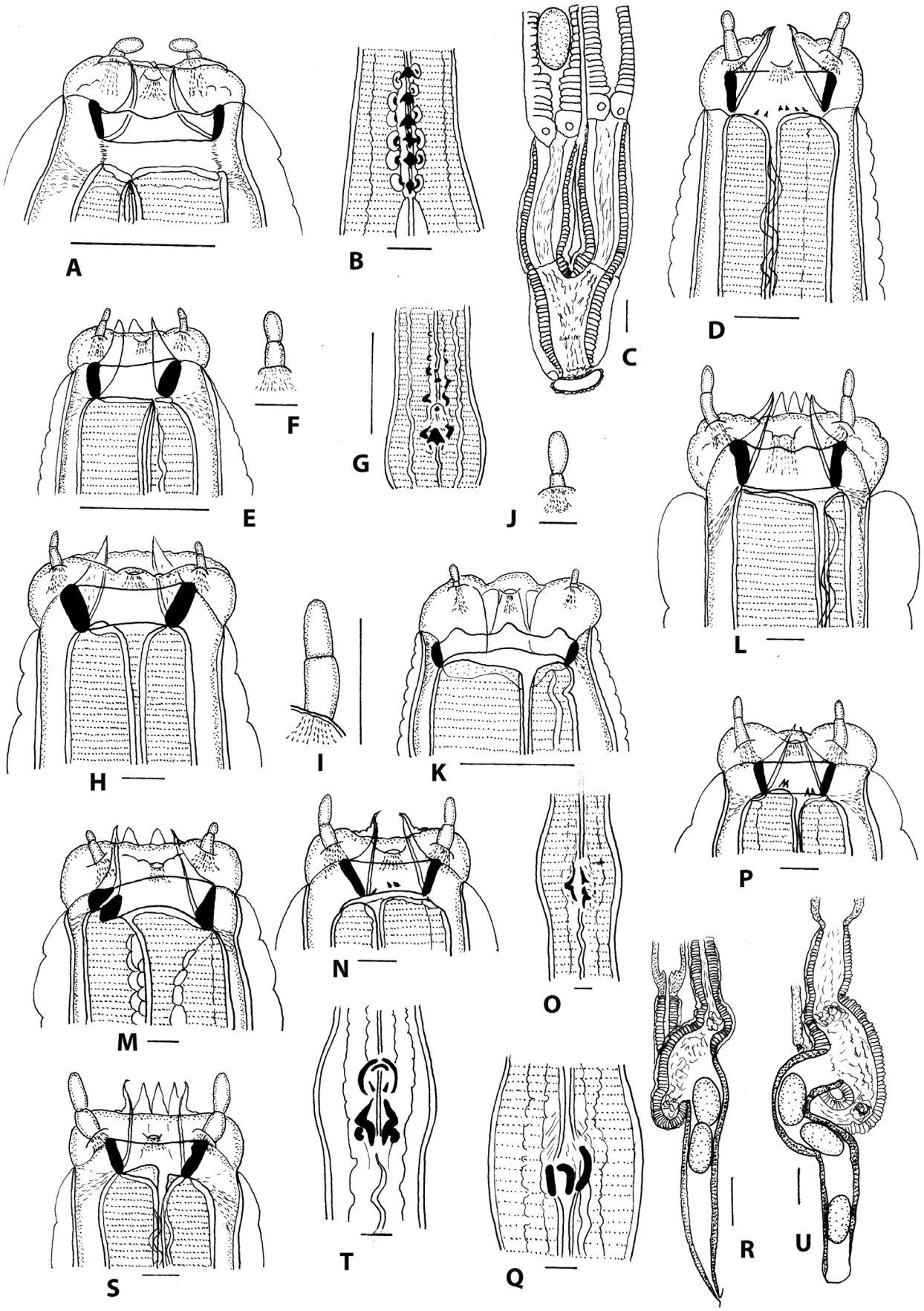
Cloacina galatea Beveridge, Jabbar & Shuttleworth, 2014, pp. 243–245, figs 23–35; Beveridge, 2016, p. 213.
Type data: holotype SAM AHC 46737, allotype SAM AHC 46738, paratypes SAM AHC 46739, BMNH 2014.2.4.5–6.
Type locality: Charters Towers, Qld (20° 05'S 146° 16'E).
Type host: *Wallabia bicolor* (Desmarest, 1804).
Site in host: stomach.
Distribution: north-eastern Qld. Map: Beveridge et al., 2014, p. 238.
Representative DNA sequence data: ITS1, ITS2: MF284700.
Diagnostic features (Fig. 9 D): Males: 3.8–4.3 mm; females 4.2–5.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses and folds; single dorsal denticle anterior to nerve ring; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in posterior oesophageal region; dorsal lobe of bursa slightly longer; branchlets of dorsal ray short; spicules 0.86–0.95 mm; spicule tip with prominent alar flange; female tail conical, slender; vagina short, straight; ovejector J-shaped.
Comment: The intended name of this species was "*C. galathea*", however in the original publication, it appeared as "*C. galatea*". Although an alternative spelling, the latter has been followed here.

Cloacina gallardi Johnston & Mawson, 1940

Cloacina gallardi Johnston & Mawson, 1940a, pp. 470–471, figs 8–11; Skrjabin et al., 1952, p. 161; Popova, 1960, pp. 21–22, fig. 11; Yamaguti, 1961, p. 400; Beveridge, 1979, p. 364; Beveridge et al., 1985, p. 387; Beveridge, 1998a, pp. 371–373, figs 422–434; Beveridge et al., 1998, p. 485; Shuttleworth et al., 2014, p. 263; Beveridge, 2016, p. 213; Spratt et al., 2017, p. 242.

Fig. 9. Genus *Cloacina*. A, *Cloacina feronia*, buccal capsule, lateral view; B, *C. feronia*, oesophageal denticles, dorsal view; C, *Cloacina frequens*, ovejector, ventral view; D, *Cloacina galatea*, buccal capsule, lateral view; E, *Cloacina gallardi*, buccal capsule, lateral view; F, *C. gallardi*, cephalic papilla; G, *C. gallardi*, oesophageal denticles, dorsal view; H, *Cloacina harriganae*, buccal capsule, lateral view; I, *C. harriganae*, cephalic papilla; J, *Cloacina hebe*, cephalic papilla; K, *C. hebe*, buccal capsule, lateral view; L, *Cloacina hecale*, buccal capsule, lateral view; M, *Cloacina hecuba*, buccal capsule, lateral view; N, *Cloacina hera*, buccal capsule, lateral view; O, *C. hera*, oesophageal denticles, lateral view; P, *Cloacina hermes*, buccal capsule, lateral view; Q, *C. hermes*, oesophageal denticles, lateral view; R, *C. hermes*, vagina, lateral view; S, *Cloacina herceus*, buccal capsule, lateral view; T, *C. herceus*, oesophageal denticles, dorsal view; U, *Cloacina hestia*, vagina, lateral view. (A–C, E–G, J–U from Beveridge, 1998a; D, from Beveridge et al., 2014; H, I, from Beveridge et al., 2019; L, from Beveridge, 2002b).

Scale-bars: A, C, E, K, R, U, 0.1 mm; B, D, F–J, L–Q, S, T, 0.01 mm.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Type data: holotype and allotype SAM V1238.
Type locality: Ourimbah, NSW (29° 17′S 143° 39′E).
Type host: *Wallabia bicolor* (Desmarest, 1804).
Other hosts: *Notamacropus dorsalis* (Gray, 1837).
Site in host: stomach.
Distribution: Qld, NSW, Vic.
Representative DNA sequence data: ITS1, ITS2: KM219853–5, 219909–11.
Diagnostic features (Figs 9 E–G): Males 9.2–13.7 mm; females 14.8–26.8 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid slightly shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; 4 groups of 3 denticles present posterior to nerve ring; nerve ring in anterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa of similar length; terminal branchlets of dorsal ray short; spicules 3.70–6.90 mm; female tail conical, short; vagina straight, elongate with few convolutions; ovejector J-shaped.
Comments: Shuttleworth et al. (2014) found very little genetic variation across the geographical range of this species.

***Cloacina harriganae* Beveridge, 2019**

Cloacina harriganae Beveridge, 2019, in Beveridge et al., 2019, pp. 460–462, figs 27–37.
Type data: holotype SAM AHC 48290, allotype SAM AHC 48291, paratypes SAM AHC 48292.
Type locality: Lake Clifton, WA (32° 48′S 115° 40′E).
Type host: *Notamacropus irma* (Jourdan, 1837).
Distribution: south-western WA.
Diagnostic features (Figs 9 H, I): Males: 3.7–6.0 mm; females 5.9–8.6 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in posterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 1.10–1.28 mm; ala diminishes gradually to spicule tip; female tail conical, slender; vagina short, straight; ovejector J-shaped.

***Cloacina hebe* Beveridge, 1998**

Cloacina hebe Beveridge, 1998a, pp. 373–375, figs 435–444; Beveridge et al., 1998, p. 485,
Type data: holotype SAM AHC 26807, allotype SAM AHC 26808, paratypes SAM AHC 26809, 27451–4.
Type locality: Rockhampton, Qld (23° 22′S 150° 32′E).
Type host: *Notamacropus dorsalis* (Gray, 1837).
Site in host: stomach.
Distribution: north-eastern Qld.
Representative DNA sequence data: ITS1, ITS2: MF284686.
Diagnostic features (Figs 9 J, K): Males: 3.2–5.6 mm; females 4.5–7.6 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule dorso-ventrally elongate, wider than long, symmetrical, anterior margin with 3 anterior projections in lateral view, 2 anterior projections in dorsal and ventral views; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid post-buccal; lobes of bursa equal; external branchlets of dorsal ray short; spicules 1.90–2.16 mm; female tail conical, slender; vagina elongate, straight; ovejector J-shaped.

***Cloacina hecale* Beveridge, 2002**

Cloacina hecale Beveridge, 2002b, pp. 11–13, figs 50–61.
Type data: holotype BMNH 1981.4506, allotype BMNH 1981.4507, paratypes BMNH 1981.4508–4535.
Type locality: Lake Trist, PNG (7° 29′S 146° 58′E).
Type host: *Dendrolagus dorianus* Ramsay, 1883.
Site in host: stomach.
Distribution: PNG.
Diagnostic features (Fig. 9 L): Males: 9.4–13.9 mm; females 19.6–22.9 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin slightly sinuous in lateral view; oesophagus without bosses, denticles and folds; nerve ring in anterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 3.90–5.05 mm; spicule tip minutely bifid; ala terminates abruptly anterior to spicule tip; female tail short, conical, stout; vagina very long, straight; ovejector J-shaped.

***Cloacina hecuba* Beveridge, 1998**

Cloacina hecuba Beveridge, 1998a, pp. 375–377, figs 445–454; Beveridge et al., 1998, p. 485.

Type data: holotype SAM AHC 26804, allotype SAM AHC 26805, paratypes SAM AHC 26806, 27455–6.

Type locality: Warrawee Station via Charters Towers, Qld (20° 18′S 146° 38′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, ITS2: MF284687.

Diagnostic features (Fig. 9 M): Males: 3.6–4.8 mm; females 4.2–5.4 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin slightly arcuate in lateral view; oesophagus with bosses extending to nerve ring; single dorsal oesophageal denticle anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; external branchlets of dorsal ray very short; spicules 1.35–1.70 mm; ala terminates gradually anterior to spicule tip; female tail short, conical; vagina short, with convolutions; ovejector J-shaped.

***Cloacina hera* Beveridge, 1998**

Cloacina hera Beveridge, 1998a, pp. 377–379, figs 455–464; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240.

Type data: holotype SAM AHC 26755, allotype SAM AHC 26756, paratypes SAM AHC 26757, 23583–4.

Type locality: Bondo State Forest, NSW (36° 21′S 149° 09′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817).

Site in host: stomach.

Distribution: Qld, NSW, Vic, SA, WA.

Diagnostic features (Figs 9 N, O): Males: 8.1–13.5 mm; females 12.0–17.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; 3 denticles at same level anterior to nerve ring; nerve ring in anterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 3.80–5.05 mm; spicule tip recurved; ala diminishes gradually to spicule tip; female tail short, conical; vagina long, sinuous; ovejector J-shaped.

Comments: The distribution of this species includes the south of Western Australia in *Mac. fuliginosus* based on collections in SAM (AHC 31793, 45583) but not published.

***Cloacina herceus* Beveridge, 1998**

Cloacina herceus Beveridge, 1998a, pp. 380–383, figs 465–477; Beveridge et al., 1998, p. 484; Arundel et al., 1990 (as *C.* cf *hydriformis*); Aussavy et al., 2011, pp. 14, 15, 16; Schultz et al., 2011, p. 238; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240; Beveridge, 2020c, p.5; 2020e, p. 204.

Type data: holotype SAM AHC 26839, allotype SAM AHC 26840, paratypes SAM AHC 23538, 27480–3.

Type locality: 70 km NE of Coonabarabran, NSW (30° 38′S 149° 35′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Lagorchestes conspicillatus* Gould, 1842; *Macropus fuliginosus* (Desmarest, 1817); *Notamacropus agilis* (Gould, 1842); *Notamacropus parryi* (Bennett, 1835); *Notamacropus rufogriseus* (Desmarest, 1817); *Osphranter robustus* (Gould, 1840); *Osphranter rufus* (Desmarest, 1822); *Petrogale assimilis* Ramsay, 1877; *Petrogale godmani* Thomas, 1923; *Petrogale inornata* Gould, 1842; *Petrogale penicillata* (Gray, 1827); *Petrogale sharmani* Eldridge & Close, 1992; *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: Qld, NSW, Vic.

Diagnostic features (Figs 9 S, T): Males: 8.4–10.9 mm; females 9.5–13.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, longer than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; 3 denticles anterior to nerve ring, dorsal denticle anterior to 2 sub-ventral denticles; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 1.51–1.67 mm; ala diminishes gradually to spicule tip; female tail short, conical; vagina short, straight; ovejector J-shaped.

Comments: Prior to 1998, this species was included within *C. hydriformis* or was referred to as *C.* cf *hydriformis*. It is limited to eastern Australia and its primary host appears to be *Mac. giganteus*. However, it has been found in much smaller numbers in a variety of other macropodids in areas in which they are sympatric with *Mac. giganteus*. The single record from *Pet. penicillata* (Schultz et al., 2011) is from a captive–bred animal released into a zone of sympatry with both grey kangaroo species.

***Cloacina hermes* Beveridge, 1998**

Cloacina hermes Beveridge, 1998a, pp. 383–385, figs 478–490; Webley et al., 2004, p. 625; Aussavy et al., 2011, pp. 14, 15; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240.

Type data: holotype SAM AHC 30179, allotype SAM AHC 30180, paratypes SAM AHC 24324, 27468–70.

Type locality: 70 km NE of Coonabarabran, NSW (30° 38′S 149° 35′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817).

Site in host: stomach.

Distribution: WA, NSW, Vic, SA, Tas.

Diagnostic features (Figs 9 P–R): Males: 7.2–9.1 mm; females 9.0–12.1 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; 3 denticles anterior to nerve ring, at same level; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 1.16–1.62 mm; spicule tip minutely bifid; ala diminishes gradually to spicule tip; female tail short, conical; vagina short, straight; ovejector J-shaped.

Comments: See *C. hestia* (below).

***Cloacina hestia* Beveridge, 1998**

Cloacina hestia Beveridge, 1998a, pp. 386–388, figs 490–502; 2020e, p. 204.

Type data: holotype SAM AHC 26758, allotype SAM AHC 26759 (previously cited as 25769), paratypes SAM AHC 24293, 27471–5, BMNH 1996.3.20.16–18, USNPC 86377.

Type locality: Glenariff, NSW (30º 47′S 146º 36′E).

Type host: *Macropus fuliginosus* (Desmarest, 1817).

Other hosts: *Macropus giganteus* Shaw, 1790.

Site in host: stomach.

Distribution: WA, NSW, Vic, SA.

Diagnostic features (Fig. 9 U): Males: 6.9–9.0 mm; females 10.6–12.9 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; 3 denticles anterior to nerve ring, at same level; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 1.92–2.35 mm; spicule tip minutely bifid; ala diminishes gradually to spicule tip; female tail short, conical; vagina short, distal vagina straight; proximal vagina sinuous ; ovejector J-shaped.

Comments: This species is very similar to *C. hermes* differing in spicule lengths, the shape of the vagina and the length of the female tail. Both occur in *Mac. fuliginosus* and *Mac. giganteus* and in some instances, both species may occur in the same individual kangaroo.

***Cloacina hobbsi* Beveridge, 2019**

Cloacina hobbsi Beveridge, 2019, in Beveridge et al., 2019, pp. 462–465, figs 38–51.

Type data: holotype SAM AHC 48265, allotype SAM AHC 48266, paratypes SAM AHC 48267.

Type locality: Lake Clifton, WA (32° 48′S 115° 40′E).

Type host: *Notamacropus irma* (Jourdan, 1837).

Distribution: south-western WA.

Representative DNA sequence data: ITS1, ITS2: MK573547, 573543.

Diagnostic features (Figs 10 A, B): Males: 3.9–4.8 mm; females 4.5–5.3 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anteriorly arcuate in lateral views, posteriorly arcuate and sinuous in dorsal and ventral views; oesophagus with bosses extending to nerve ring; comb-like structure in pre-neural swelling; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; external branchlets of dorsal ray short; spicules 1.60–1.90 mm; ala diminishes gradually to spicule tip, continues as flange surrounding tip; female tail conical, slender; vagina short, straight; ovejector J-shaped.

***Cloacina hydriformis* Johnston & Mawson, 1938**

Cloacina hydriformis Johnston & Mawson, 1938, p. 273, figs 28–31; Skrjabin et al., 1952, p.161; Popova, 1960, pp. 22–23, fig. 12; Yamaguti, 1961, p. 400; Mykytowykz, 1964, p. 682; Beveridge et al., 1989, p. 276; Arundel et al., 1990, p. 370; Beveridge, 1998a, pp. 389–391, figs 503–513; Beveridge et al., 1998, p. 485; Beveridge, 2020c, p. 5; 2020e, p. 204.

Type data: syntypes SAM V1364, paratypes SAM AHC 1841, S1015.

Type locality: Mount Liebig, NT (23° 19′S 131° 22′E).

Type host: *Petrogale lateralis* Gould, 1840 (MacDonnell Ranges race).

Other hosts: *Macropus fuliginosus* (Desmarest, 1817); *Macropus giganteus* Shaw, 1790; *Osphranter robus*tus (Gould, 1840); *Osphranter rufus* (Desmarest, 1822); *Petrogale purpureicollis* Le Souef, 1924; *Petrogale xanthopus* Gray, 1855.

Site in host: stomach.

Distribution: NT, Qld, NSW, SA, WA.

Representative DNA sequence data: 18S, 28S, ITS: KJ776347, 851977–81 (not Y10796, identified in Genbank as *C. hydriformis*, but is in fact *C. herceus*).

Diagnostic features (Fig. 10 C): Males: 5.4–9.2 mm; females 7.6–11.6 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 1.41–1.66 mm; ala terminates abruptly anterior to spicule tip; female tail conical; vagina short, straight; ovejector J-shaped.

Comments: Most records of this nematode are from *O. rufus* with other records appearing to be incidental infections in sympatric host species. In the past, a number of species have been incorrectly included under this name. Collections in SAM are labelled as "syntypes" (containing 2 males and 2 females) and "paratypes"(containing 5 males and 14 females as well as a slide preparation) respectively for reasons unknown.

***Cloacina hylas* Beveridge, 2019**

Cloacina hylas Beveridge, 2019, pp. 193–196, figs 11–21.

Type data: holotype SAM AHC 48304, allotype SAM AHC 48305, paratypes SAM AHC 48306–7.

Type locality: Battery Creek, 20 km N of Bowen, Qld (20º 01′S 148º 15′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

Distribution: north-eastern Qld.

Diagnostic features (Fig. 10 D): Males: 2.5–3.1 mm; females 3.2–4.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa slightly longer than lateral lobes; external branchlets of dorsal ray short; spicules 0.73–0.84 mm, tip slightly enlarged; ala diminishes gradually to spicule tip; female tail conical; vagina very short, straight; ovejector J-shaped.

***Cloacina hyperaea* Beveridge, 2002**

Cloacina hyperaea Beveridge, 2002b, pp. 13–15, figs 62–74.

Type data: holotype SAM AHC 31442, allotype SAM AHC 31443, paratypes SAM AHC 31444, BMNH 2001.4.10.7–8, USNPC 91136.

Type locality: Usino, Madang, PNG (5° 32′S 145° 23′E).

Type host: *Dorcopsis hageni* Heller, 1897.

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 10 E, F): Males: 4.2–5.1 mm; females 5.3–6.1 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anteriorly arcuate in lateral views, posteriorly arcuate in ventral views, sinuous in dorsal view with anterior arch around dorsal oesophageal tooth; oesophagus with bosses extending to nerve ring; single dorsal denticle anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid at level of nerve ring; lobes of bursa equal; external branchlets of dorsal ray short; spicules 2.25–2.49 mm; ala diminishes gradually to spicule tip; female tail conical, slender; vagina elongate, distal vagina straight, proximal vagina shortly reflexed; ovejector J-shaped.

***Cloacina hypsipyle* Beveridge, 1998**

Cloacina hypsipyle Beveridge, 1998a, pp. 391–393, figs 514–524; Beveridge et al., 1998, p. 485.

Type data: holotype SAM AHC 26760, allotype SAM AHC 26761, paratypes SAM AHC 26762.

Type locality: Logan Village, Qld (27° 46′S 153° 06′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

Distribution: eastern Qld.

Diagnostic features (Fig. 10 G): Males 3.6–4.1mm; females 4.1–5.3 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical, very short; distal segment elongate, ovoid, much longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule slightly wider than long, symmetrical, anterior margin sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa equal; external branchlets of dorsal ray short; spicules 1.04–1.15 mm; female tail conical, slender; vagina straight; ovejector J-shaped.

***Cloacina idas* Beveridge, 2019**

Cloacina idas Beveridge, 2019, pp. 196–199, figs 22–32.

Type data: holotype SAM AHC 48314, allotype SAM AHC 48315, paratypes SAM AHC 31021, 31118.

Type locality: Mount Elephant, Cooktown, Qld (16º 27′S 144º 56′E).

Type host: *Petrogale godmani* Thomas, 1923.

Site in host: stomach.

Distribution: north-eastern Qld.

Diagnostic features (Figs 10 H–J): Males 3.8–4.2 mm; females 3.6–5.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight, walls arcuate; oesophagus without bosses and folds; single dorsal denticle anterior to nerve ring; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; spicules 1.52–1.80 mm; ala diminishes gradually to tip; female tail conical; vagina convoluted; ovejector J-shaped.

Cloacina inflata* Johnston & Mawson, 1938 *species inquirenda

Cloacina inflata Johnston & Mawson, 1938, pp. 285–286, figs 77–80; Skrjabin et al., 1952, p. 161; Popova, 1960, pp. 24–25, fig. 13; Yamaguti, 1961, p. 400; Mykytowykz, 1964, p. 682; Beveridge, 1998a, pp. 501–502.

Type data: holotype and allotype SAM V1353,

Type locality: Mount Liebig, NT (23° 19′S 131° 22′E).

Type host: *Osphranter rufus* (Desmarest, 1822).

Comments: Beveridge (1998a) re–examined the type specimens but concluded that due to their poor state of preservation, specific identification was not possible. The shape of the cephalic papillae suggests that the species belongs with the species group *C. daveyi, C. epona*, *C. frequens*, and *C. feronia,* all primarily parasites of *O. robustus* rather than *O. rufus*. No similar specimens have been found in *O. rufus* in subsequent studies (Beveridge, 2020e) suggesting the possibility of mistaken host identification.

***Cloacina io* Beveridge, 1998**

Cloacina io Beveridge, 1998a, pp. 393–395, figs 525–537; Beveridge et al., 1998, p. 485; Beveridge, 2016, p. 213; 2020f, pp. 215–223.

Type data: holotype SAM AHC 26763, allotype SAM AHC 26764, paratypes SAM AHC 26765, BMNH 1996.3.20.21–22, USNPC 86378.

Type locality: Shute Harbour, Qld (20º 16′S 148º 43′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Other hosts: *Notamacropus dorsalis* (Gray, 1837); *Petrogale assimilis* Ramsay, 1877.

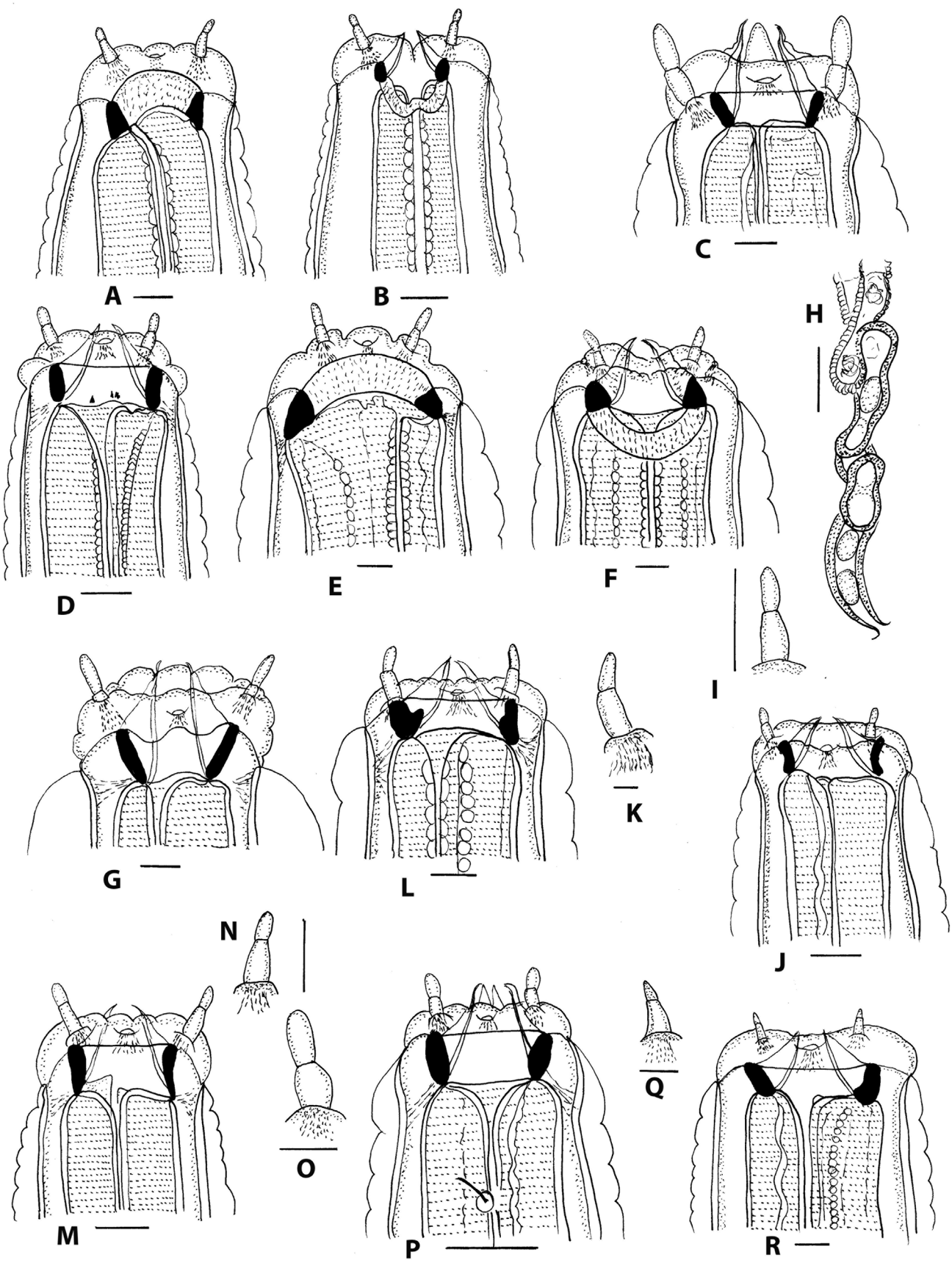
Site in host: stomach.

Distribution: north-eastern Qld.

Representative DNA sequence data: ITS1, ITS2: KM219856, 219926.

Fig. 10. Genus *Cloacina*. A, *Cloacina hobbsi*, buccal capsule, lateral view; B, *C. hobbsi*, buccal capsule, dorsal view; C, *Cloacina hydriformis*, buccal capsule, lateral view; D, *Cloacina hylas*, buccal capsule, lateral view; E, *Cloacina hyperaea*, buccal capsule, lateral view; F, *C. hyperaea*, buccal capsule, ventral view; G, *Cloacina hypsipyle*, buccal capsule, lateral view; H, *Cloacina idas*, vagina, lateral view; I, *C. idas*, cephalic papilla; J, *C. idas*, buccal capsule, lateral view; K, *Cloacina io*, cephalic papilla; L, *C. io*, buccal capsule, lateral view; M, *Cloacina ips*, buccal capsule, lateral view; N, *C. ips*, cephalic papilla; O, *Cloacina ixion*, cephalic papilla; P, *C. ixion*, buccal capsule, lateral view; Q, *Cloacina johnstoni*, cephalic papilla; R, *C. johnstoni*, buccal capsule, lateral view. (A, B, from Beveridge et al, 2019; C, G, K–P, from Beveridge, 1998a; D, H–J from Beveridge, 2019; E, F from Beveridge, 2002b; Q, R from Shuttleworth et al., 2016a).

Scale-bars: H, 0.1 mm; A–G, I–R, 0.01 mm.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Diagnostic features (Figs 10, K, L): Males: 3.4–4.5 mm; females 3.8–4.7 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment bulbous; distal segment slender, cylindrical, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring, single dorsal oesophageal denticle anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 1.27–1.44 mm; female tail conical; vagina short; ovejector J-shaped.

Comments: This is an uncommon species, having been found on single occasions in *N. dorsalis*, *Pet. assimilis* and *Wal. bicolor* in Queensland.

***Cloacina ips* Beveridge, 1998**

Cloacina ips Beveridge, 1998a, pp. 395–397, figs 538–548; Beveridge et al., 1998, p. 485.

Type data: holotype SAM AHC 26766, allotype SAM AHC 26767.

Type locality: Kirrama, Qld (18º 09'S 145º 37'E).

Type host: *Notamacropus parryi* (Bennett, 1835).

Site in host: stomach.

Distribution: north-eastern Qld.

Diagnostic features (Figs 10 M, N): Males: 3.8–5.8 mm; females 3.8–4.6 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; external branchlets of dorsal ray arise anterior to principal bifurcation; spicules 1.36–1.40 mm; female tail conical; vagina short, straight; ovejector J-shaped.

***Cloacina ixion* Beveridge, 1998**

Cloacina ixion Beveridge, 1998a, pp. 397–399, figs 549–562; Beveridge et al., 1998, p. 485; Beveridge, 2020c p. 5; 2020e, p. 204.

Type data: holotype SAM AHC 26768, allotype SAM AHC 26769, paratypes SAM AHC 26770, 27494–7, BMNH 1996.3.20.23–24, USNPC 96379.

Type locality: Lissadell Station via Kununurra, WA (16º 41'S 128º 33'E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Notamacropus parryi* (Bennett, 1835); *Osphranter antilopinus* (Gould, 1842); *Osphranter rufus* (Desmarest, 1822).

Site in host: stomach.

Distribution: WA (Kimberley Division; Pilbara), NT (Top End), north-eastern Qld.

Representative DNA sequence data: ITS1, ITS2: KU 853831, 853852, 853863, 853904.

Diagnostic features (Figs 10 O, P): Males: 8.7–12.9 mm; females 10.3–13.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment doliiform; distal segment bulbous, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; 3 denticles anterior to nerve ring, dorsal denticle anterior to 2 sub-ventral denticles; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 3.81–4.50 mm; ala diminishes gradually to spicule tip; female tail short, conical; vagina elongate, sinuous; ovejector J-shaped.

Comments: This species is very similar to *C. magnipapillata* with which it has been confused (Mawson, 1961a). The morphological differences are subtle, with the distal segment of the cephalic papillae being globose in *C. ixion* and cylindrical in *C. magnipapillata*, together with differences in the shape of the buccal capsule and spicule lengths (Beveridge, 1998a). The morphological differences are however supported by DNA sequence data (Chilton et al., 2017).

***Cloacina johnstoni* Shuttleworth, Jabbar & Beveridge, 2016**

Cloacina johnstoni Shuttleworth, Jabbar & Beveridge, 2016b, pp. 3358–3360, figs 1–12; Shuttleworth et al, 2016a, p. 247; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 47659, allotype SAM AHC 47660, paratypes SAM AHC 47661, BMNH 2015.9.10.1–2.

Type locality: Mulga Park Station via Alice Springs, NT (25º 63'S 131º 79'E).

Type host: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: WA, NT, Qld, SA. Map: Shuttleworth et al., 2016b. p. 3361.

Representative DNA sequence data: ITS1, ITS2: KU853837, 853919–21, 853923, 863946.

Diagnostic features (Figs 10 Q, R): Males: 6.2–7.6 mm; females 7.3–9.7 mm; cervical cuticle not inflated; cephalic papillae short: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, slightly asymmetrical, anterior margin straight in lateral view; dorsal oesophageal tooth projects into buccal capsule; oesophagus with faint bosses extending to nerve ring, terminating in faint, comb-like striations; folds and denticles absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray sub-equal; spicules 2.95–4.10 mm; ala diminishes gradually to spicule tip; female tail short, conical; vagina elongate, recurrent; ovejector J-shaped.

Comments: This species is most similar to *C. macropodis* with which it is often synhospitalic. The most obvious difference between the two species is the much smaller cephalic papillae in *C. johnstoni*. The two species are clearly differentiable based on molecular data and phylogenetically are sister species to one another (Chilton et al., 2017).

***Cloacina kartana* Mawson, 1975**

Cloacina kartana Mawson, 1975, pp. 40–41, figs 8–14; Smales & Mawson, 1978a, p.11; Beveridge, 1998a, pp. 400–401, figs 563–575.

Type data: holotype and allotype SAM V1266.

Type locality: Kangaroo Island, SA (35º 51′S 137º 10′E).

Type host: *Notamacropus eugenii* (Desmarest, 1817).

Site in host: stomach.

Distribution:, SA (Kangaroo Island), south-western WA.

Diagnostic features (Figs 11 A–C): Males: 7.3–9.4 mm; females 10.0–14.6 mm; cervical cuticle not inflated; cephalic papillae short: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight in lateral view; oesophagus without bosses and folds; 3 denticles present posterior to nerve ring; 2 sub-ventral denticles anterior to single dorsal denticle; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid at level of nerve ring; lobes of bursa equal; branchlets of dorsal ray short; spicules 1.37–1.55 mm; female tail short, conical; vagina short, straight; ovejector J–shaped.

Comments: This species is unique in having three denticles immediately posterior to the nerve ring with the two sub-ventral denticles anterior to the single dorsal denticle. Apart from published records, specimens in SAM AHC (31950) indicate that the species also occurs in the Perup River region in the southwest of WA.

***Cloacina laius* Beveridge, 1999**

Cloacina laius Beveridge, 1999b, pp. 20–22, figs 15–28; Beveridge et al., 2019, pp. 465–467, figs 52–59.

Type data: holotype SAM AHC 30567, allotype SAM AHC 30568, paratypes SAM AHC 30569, BMNH 1998.9.28.9–10.

Type locality: Rottnest Island, WA (32º 01′S 115º 30′E).

Type host: *Setonix brachyurus* (Quoy & Gaimard, 1830)

Other hosts: *Notamacropus irma* (Jourdan, 1837).

Site in host: stomach.

Distribution: south-western WA.

Diagnostic features (Fig. 11 D): Males 5.6–7.4 mm; females 7.3–9.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; mouth dorso-ventrally elongate; buccal capsule wider than long, symmetrical, anteriorly arcuate in lateral view, posteriorly arcuate in dorsal and ventral views; oesophagus with bosses extending to nerve ring; single dorsal denticle present anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid at level of nerve ring; lobes of bursa equal; external branchlets of dorsal ray short; spicules 1.50–1.97 mm; female tail short, conical; vagina short, recurrent; ovejector J-shaped.

Comments: Originally described from *Set. brachyurus*, this species has subsequently been found commonly in the sympatric *N. irma* in Western Australia (Beveridge et al., 2019). Which is the primary host remains to be determined.

***Cloacina leto* Beveridge, 1998**

Cloacina leto Beveridge, 1998a, pp. 402–404, figs 576–589; Beveridge et al., 1998, p. 485; Spratt et al., 2017, p. 240.

Type data: holotype SAM AHC 26777, allotype SAM AHC 26778, paratypes SAM AHC 26779, 27502–3.

Type locality: Woodstock, Qld (19º 35′S 146º 50′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Lagorchestes conspicillatus* Gould, 1842; *Notamacropus agilis* (Gould, 1842).

Site in host: stomach.

Distribution: eastern Qld, NSW, Vic.

Diagnostic features (Fig. 11 F): Males 4.6–8.1 mm; females 7.7–9.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, slightly asymmetrical with dorsal wall shorter and thicker than ventral wall; anterior margin of buccal capsule straight; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring; single dorsal denticle present anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; external branchlets of dorsal ray short; spicules 2.80–3.24 mm; female tail slender, conical; vagina elongate, convoluted; ovejector J-shaped.

Comments: This species appears to be primarily a parasite of *Mac. giganteus* along the eastern coast of Australia. Occurrences in *La. conspicillatus* and *N. agilis* appear to be incidental infections in areas of host sympatry.

***Cloacina liebigi* Johnston & Mawson, 1938**

Cloacina liebigi Johnston & Mawson, 1938, pp. 284–285, figs 73–76; Skrjabin et al., 1952, p. 161; Popova, 1960, pp. 25–26, fig. 14; Yamaguti, 1961, p. 400; Mykytowykz, 1964, p. 682; Beveridge, 1998a, pp. 404–406, figs 590–600; 2020e, p. 204.

Type data: holotype and allotype SAM V1363.

Type locality: Mount Liebig, NT (23° 19′S 131° 22′E).

Type host: *Osphranter rufus* (Desmarest, 1822).

Other hosts: *Macropus fuliginosus* (Desmarest, 1817).

Site in host: stomach.

Distribution: NT, Qld, NSW, SA, WA.

Representative DNA sequence data: 18S, 28S, ITS: KJ776348–50 cox1: KJ851927–9.

Diagnostic features (Fig. 11 G): Males 11.2–14.2 mm; females 14.3–19.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 4.00–5.42 mm; female tail conical; vagina elongate, recurrent; ovejector J-shaped.

Comments: The primary host of this species is *O. rufus,* with the single record from *Mac. fuliginosus* apparently being an incidental infection in a sympatric host species.

***Cloacina linstowi* Johnston & Mawson, 1940**

Cloacina linstowi Johnston & Mawson, 1940a, pp. 469–470, figs 5–7; Skrjabin et al., 1952, p. 161; Popova, 1960, pp. 26–27, fig. 15; Yamaguti, 1961, p. 300; Beveridge, 1998a, pp. 406–408, figs 601–612; Beveridge et al., 1998, p. 485.

Type data: syntypes SAM V1284.

Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Other hosts: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

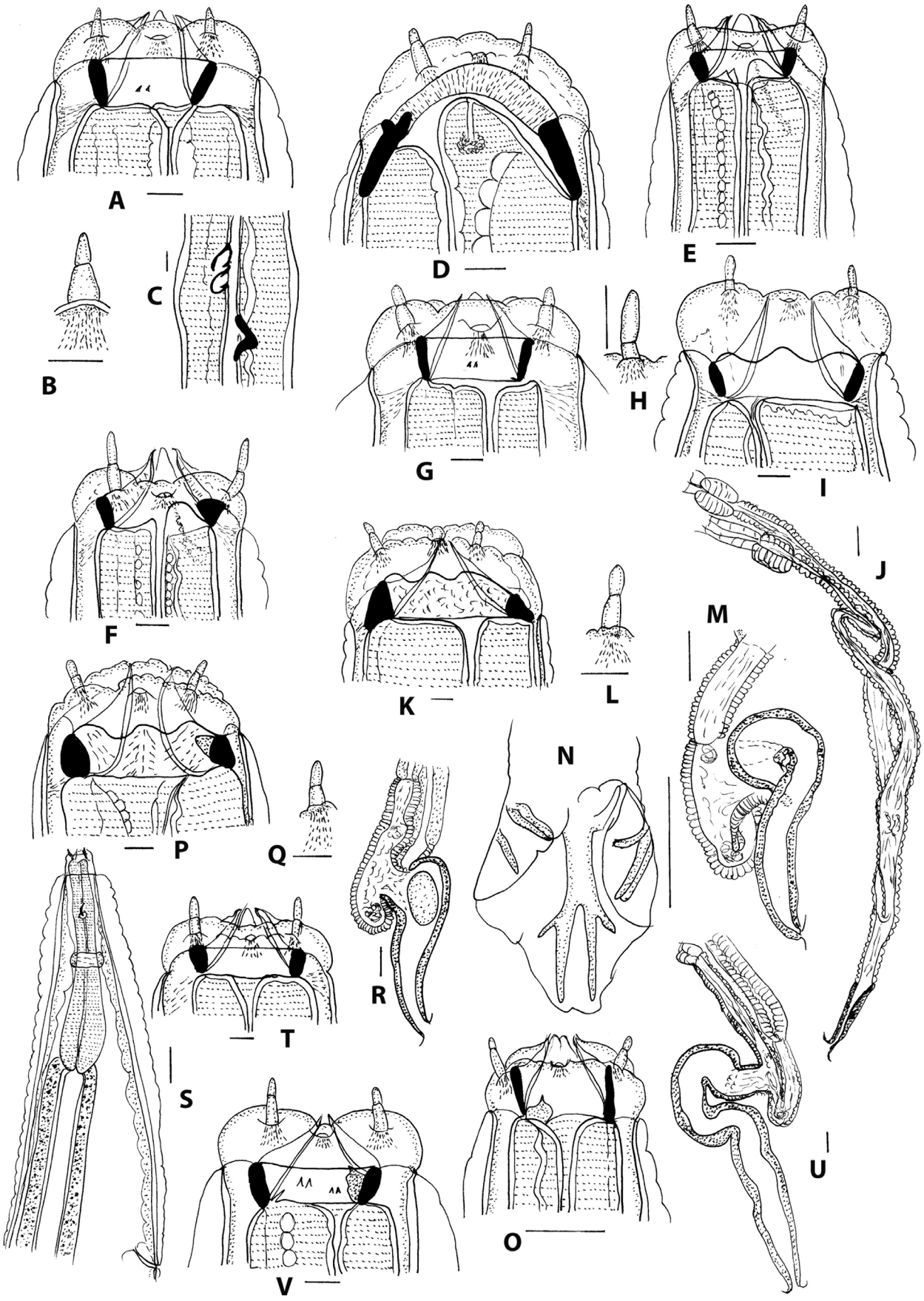
Distribution: eastern Qld.

Representative DNA sequence data: ITS1, ITS2: MF284688.

Diagnostic features (Figs 11 H–J): Males 4.7–7.3 mm; females 4.3–5.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of

Fig. 11. Genus *Cloacina*. A, *Cloacina kartana*, buccal capsule, lateral view; B, *C. kartana*, cephalic papilla; C, *C. kartana*, oesophageal denticles, lateral view; D, *Cloacina laius*, buccal capsule, lateral view; E. *Cloacina littoralis*, buccal capsule, lateral view; F, *Cloacina leto*, buccal capsule, lateral view; G, *Cloacina liebigi*, buccal capsule, lateral view; H, *Cloacina linstowi*, cephalic papilla; I, *C. linstowi*, buccal capsule, lateral view; J, *C. linstowi*, vagina and ovejector; K, *Cloacina lityerses*, buccal capsule, lateral view; L, *C. lityerses*, cephalic papilla; M, *C. lityerses*, vagina and ovejector, lateral view; N, *Cloacina longibursata*, bursa, ventral view; O, *C. longibursata*, buccal capsule, lateral view; P, *Cloacina longelabiata*, buccal capsule, lateral view; Q, *C. longelabiata*, cephalic papilla; R, *C. longelabiata*, vagina and ovejector, lateral view; S, *Cloacina longispiculata,* anterior end, lateral view; T, *C. longispiculata*, buccal capsule, lateral view; U, *C. longispiculata*, vagina and ovejector, lateral view; V, *Cloacina macropodis*, buccal capsule, lateral view. (A–C, E–M, P–V from Beveridge, 1998a; D from Beveridge, 1999b; N, O from Beveridge et al., 2018).

Scale-bars: J, M, N, R, S, U, 0.1 mm; A–I, K, L, O–Q, T, V, 0.01 mm.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buccal capsule sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa equal; branchlets of dorsal ray short; spicules 0.70–0.85 mm; female tail conical; vagina short, straight; ovejector Y-shaped; infundibulum very long; sphincter present between infundibulum and uterus.

Comments: Although initially described from *N. rufogriseus*, this species has never since been found in the type host, but is common in the related species *N. dorsalis* (Beveridge et al., 1998). The two host species are superficially quite similar and this may represent a case of mistaken host identification.

***Cloacina littoralis* Beveridge, 1998**

Cloacina littoralis Beveridge, 1998a, pp. 409–410, figs 613–624; Aussavy et al., 2011, p. 17; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 213.

Type data: holotype SAM AHC 26771, allotype SAM AHC 26772, paratypes SAM AHC 26773, 27511–2, BMNH 1996.2.21.3–4, USNPC 86382.

Type locality: Wye River, Vic (38º 39'S 143º 54'E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: Vic.

Diagnostic features (Fig. 11 E): Males 3.6–4.2 mm; females 3.8–4.4 mm; cervical cuticle very slightly inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, as long as proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule straight; prominent dorsal oesophageal tooth and 2 smaller subventral teeth project into buccal capsule; oesophagus with bosses extending to nerve ring; denticles and folds absent; nerve ring in posterior oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; branchlets of dorsal ray short; spicules 0.88–0.95 mm; ala diminishing in width towards tip; female tail conical; vagina short, straight; ovejector J-shaped.

***Cloacina lityerses* Beveridge, 1998**

Cloacina lityerses Beveridge, 1998a, pp. 411–413, figs 625–634.

Type data: holotype SAM AHC 26775, allotype SAM AHC 26776, paratypes SAM AHC 1847, 3083, 3087, 27513–5.

Type locality: Mount Liebig, NT (23° 19'S 131° 22'E).

Type host: *Petrogale lateralis* Gould, 1840 (MacDonnell Ranges race).

Site in host: stomach.

Distribution: southern NT, northern SA.

Diagnostic features (Figs 11 K–M): Males 5.1–7.9 mm; females 8.7–10.2 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, as long as proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, asymmetrical with dorsal wall much shorter than ventral wall; anterior margin of buccal capsule sinuous; prominent dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses in anterior region; denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes similar; branchlets of dorsal ray very short; spicules 2.30–2.56 mm; ala diminishing in width towards tip; female tail short, conical; vagina short, recurrent; ovejector J-shaped.

***Cloacina longelabiata* Johnston & Mawson, 1939**

Cloacina minor Johnston & Mawson, 1938, pp. 283–284, figs 63–66; Skrjabin et al., 1952, p. 161; Popova, 1960, pp. 30–31, fig. 18.

Cloacina longelabiata Johnston & Mawson, 1939c, p. 209, 1940b, p.97; Yamaguti, 1961, p. 400; Beveridge, 1998a, pp. 413–415, figs 635–645; Shuttleworth et al., 2016a, pp. 246–247; Beveridge, 2020, p. 5.

Type data: holotype, allotype SAM V1360.

Type locality: Mount Liebig, NT (23° 19'S 131° 22'E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Petrogale lateralis* Gould, 1840 (MacDonnell Ranges race).

Site in host: stomach.

Distribution: southern NT, north-western Qld, northern SA.

Representative DNA sequence data: ITS1, ITS2: KU853837–8, 853851, 853926, 853945, 853948–50.

Diagnostic features (Figs 11 P–R): Males 5.3–8.9 mm; females 9.3–12.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, as long as proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, asymmetrical with dorsal wall much shorter than ventral wall; anterior margin of buccal capsule sinuous; prominent dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses in anterior region; denticles and folds absent; nerve ring in mid-oesophageal region; excretory

pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; bursal lobes similar; branchlets of dorsal ray very short; spicules 1.18–1.45 mm; female tail short, conical; vagina short, straight; ovejector J-shaped.

***Cloacina longibursata* Beveridge, 2018**

Cloacina longibursata Beveridge, 2018 in Beveridge, et al., 2018, pp. 532–534, figs 12–21; Beveridge, 2020, p. 5.

Type data: holotype SAM AHC 48096, allotype SAM AHC 48097, paratypes SAM AHC 48098.

Type locality: 70 km S of Maningrida, NT (12° 03′S 134° 13′E).

Type host: *Osphranter antilopinus* (Gould, 1842).

Other hosts: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: NT (TopEnd).

Diagnostic features (Figs 11 N, O.): Males 3.4–3.8 mm; females 3.2–6.2 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule straight; prominent dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa much longer than lateral lobes; external branchlets of dorsal ray very short, internal branchlets long; spicules 1.35–1.47 mm; ala diminished gradually towards tip; female tail short, conical; vagina short, straight; ovejector J-shaped.

Comment: The illustrations to this species are incorrectly labelled as "*longibursaris*" in the original publication (Beveridge et al., 2018).

***Cloacina longispiculata* Johnston & Mawson, 1939**

Cloacina longispiculata Johnston & Mawson, 1939a, pp. 129, 131–132, figs 25–28; Skrjabin et al., 1952, p. 161; Popova, 1960, p. 27; Mawson, 1961b, p. 89, figs 6–7; Yamaguti, 1961, p. 400; Speare et al., 1983, p. 90; Beveridge, 1998a, pp. 415–417, figs 646–654; Beveridge et al., 1998, p. 485.

Type data: syntypes SAM V1550, SAM AHC 21659–61.

Type locality: Gregory River, Qld (19° 08′S 138° 17′E).

Type host: *Notamacropus agilis* (Gould, 1842).

Site in host: stomach.

Distribution: north Qld, NT (Top End), WA (Kimberley Division).

Diagnostic features (Figs 11 S–U): Males 8.8–13.2 mm; females 13.6–18.8 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, as long as proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule straight; oesophagus without bosses and folds; single dorsal denticle at level of nerve ring; nerve ring in mid-oesophageal region; excretory pore well posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 3.8–4.47 mm; ala diminishes gradually towards tip; female tail short, conical; vagina short, deviated prior to entry into ovejector; ovejector J-shaped.

***Cloacina macropodis* Johnston & Mawson, 1938**

Cloacina macropodis Johnston & Mawson, 1938, pp. 278–279, figs 47–50; 1939a, pp. 122, 133; 1939b, p. 553; 1940b, p.97; Skrjabin et al., 1952, p. 161; Popova, 1960, pp. 27–28, fig. 16; Yamaguti, 1961, p. 400; Arundel et al., 1979, pp. 365, 370; Beveridge, 1998a, pp. 418–420, figs 655–668; Beveridge et al., 1998, p. 485; Shuttleworth et al., 2016a, p. 247; Beveridge, 2020c, p. 5; 2020e, p. 240.

Type data: holotype, allotype SAM V1356, paratypes SAM AHC 25299.

Type locality: Mount Liebig, NT (23° 19′S 131° 22′E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Macropus fuliginosus* (Desmarest, 1817); *Notamacropus parryi* (Bennett, 1835); *Osphranter antilopinus* (Gould, 1842); *Osphranter rufus* (Desmarest, 1822); *Petrogale xanthopus* Gray, 1855 (captive).

Site in host: stomach.

Distribution: WA, NT, Qld, NSW, SA.

Representative DNA sequence data: ITS1, ITS2: KU853834, 853842, 853856, 853870, 853879, 853881, 853885, 853922, 853932, 85393–8, 853940, 853952–3.

Diagnostic features (Fig. 11 V): Males 6.5–9.1 mm; females 6.8–11.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule straight; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses in anterior region; denticles absent but small comb-like structure present anterior to nerve ring; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 2.7–3.1 mm;

ala diminishes gradually towards tip; female tail conical; vagina elongate, prominently recurrent; ovejector J-shaped.

Comments: Early papers (cited above) listed various hosts for this species but not all have been confirmed. *Osphranter robustus* appears to be the usual host with occasional infections in sympatric species. Its ability to infect additional species is shown by its occurrence in a captive population of *Pet. xanthopus* in the Adelaide Zoo, SA.

***Cloacina magnipapillata* Johnston & Mawson, 1939**

Cloacina magnipapillata Johnston & Mawson, 1939b, p. 530, figs 49–52; 1939d, p. 307; Skrjabin et al., 1952, p. 161; Popova, 1960, pp. 29–30, fig. 17; Yamaguti, 1961, p. 401; Arundel et al., 1979, pp. 370; Beveridge & Arundel, 1979, p. 72; Beveridge, 1998a, pp. 421–424, figs 669–682; Beveridge et al., 1998, p. 485; Webley et al., 2004, p. 629.

Type data: syntypes SAM V1566.

Type locality: Coonamble, NSW (30º 57′S 148º 24′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817); *Notamacropus agilis* (Gould, 1842); *Notamacropus parryi* (Bennett, 1835).

Site in host: stomach.

Distribution: Qld, northern and western NSW, north-western Vic, SA, south-western WA.

Diagnostic features (Figs 12 A–D): Males 8.3–12.6 mm; females 12.5–18.5 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule straight; dorsal oesophageal tooth present but not prominent; oesophagus without bosses and folds; 3 denticles, dorsal denticle anterior to sub-ventral denticles, anterior to nerve ring; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal juncton; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 3.10–3.65 mm; ala diminishing gradually towards spicule tip; female tail conical; vagina elongate, prominently sinuous; ovejector J-shaped.

Comments: Based on current collections, this species is primarily parasitic in the two species of grey kangaroos, *Mac. fuliginosus* and *Mac. giganteus*. However, it is noticeably lacking in the south-eastern part of the range of *Mac. giganteus* (Beveridge, 1998a). Records from *N. agilis* and *N. parryi* appear to be incidental infections in areas of host sympatry. Beveridge (1998a) noted differences in the mean spicule lengths of specimens from the two species of grey kangaroos suggesting that additional species may be involved.

***Cloacina maia* Beveridge, 1998**

Cloacina maia Beveridge, 1998a, pp. 424–426, figs 683–693; Beveridge et al., 1998, p. 485.

Type data: holotype SAM AHC 26816, allotype SAM AHC 26817.

Type locality: Rockhampton, Qld (23º 22′S 150º 32′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

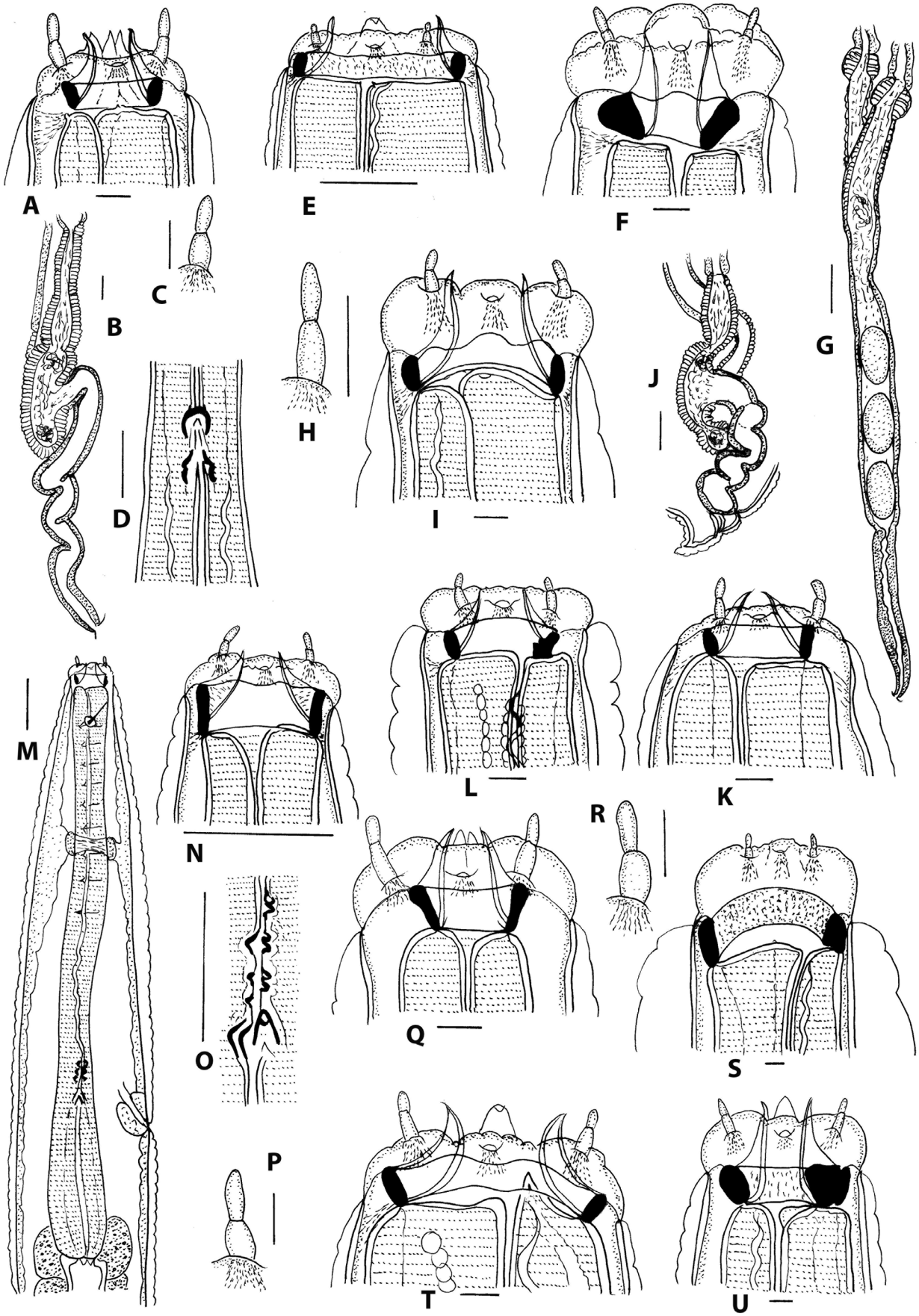
Site in host: stomach.

Distribution: north-eastern Qld.

Diagnostic features (Figs 12 F, G): Males 4.1–4.2 mm; females 4.8–5.6 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment cylindrical; distal segment slender, elongate, longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 1.97–2.25 mm; ala terminates abruptly anterior to spicule tip; female tail conical; vagina elongate; ovejector Y-shaped; sphincter present between infundibulum and uterus.

Fig. 12. Genus *Cloacina*. A, *Cloacina magnipapillata*, buccal capsule, lateral view; B, *C. magnipapillata*, vagina, lateral view; C, *C. magnipapillata*, cephalic papilla; D, *C. magnipapillata*, oesophageal denticles, dorsal view; E, *Cloacina mawsonae*, buccal capsule, lateral view; F, *Cloacina maia*, buccal capsule, lateral view; G, *C. maia*, vagina and ovejector, lateral view; H, *Cloacina middletoni*, cephalic papilla; I, *C. middletoni*, buccal capsule, lateral view; J, *Cloacina metis*, posterior end of female, lateral view; K, *C. metis,* buccal capsule, lateral view; L, *Cloacina minor*, buccal capsule, lateral view; M, *Cloacina niobe*, oesophagus, lateral view; N, *C. niobe*, buccal capsule, lateral view; O, *C. niobe*, oesophageal denticles, lateral view; P, *C. niobe*, cephalic papilla; Q, *Cloacina nike*, buccal capsule, lateral view; R, *Cloacina nephele*, cephalic papilla; S, *C. nephele*, buccal capsule, lateral view; T, *Cloacina mundayi*, buccal capsule, lateral view; U, *Cloacina obtusa*, buccal capsule, lateral view. (A–G, J–Q, T, U, from Beveridge, 1998a; H, I, from Beveridge et al., 2019; R, S, from Beveridge, 2002b).

Scale-bars: B, G, J, M, N, O, 0.1 mm; A, C–F, H, I, K, L, P–U, 0.01 mm.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***Cloacina mawsonae* Beveridge, 1979**

Cloacina mawsonae Beveridge, 1979, pp. 364–367, figs 1–12; Beveridge et al., 1985, p. 378; Beveridge, 1998a, pp. 426–429, figs 694–703; Beveridge et al., 1998, p. 486; Aussavy et al., 2011, p. 17; Shuttleworth et al., 2014, p. 263; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 213; Spratt et al., 2017, p. 242.

Type data: holotype SAM V1619, allotype SAM V1620, paratypes SAM V1621–4.

Type locality: Bonang, Vic. (37º 11′S 148º 44′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: eastern Qld, eastern NSW, Vic.

Representative DNA sequence data: ITS1, ITS2: KM219858–60, 219906–8.

Diagnostic features (Fig. 12 E): Males 5.0–9.2 mm; females 4.7–11.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule much wider than long, symmetrical; anterior margin of buccal capsule slightly sinuous; oesophagus without bosses, denticles and folds, sub-cylindrical; nerve ring in posterior oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 2.20–2.62 mm; female tail short, conical; vagina elongate, straight; ovejector J-shaped.

***Cloacina metis* Beveridge, 1998**

Cloacina metis Beveridge, 1998a, pp. 429–430, figs 704–712.

Type data: holotype SAM AHC 26821, allotype SAM AHC 2682, paratypes SAM AHC 26823–4, BMNH 1996.3.21.5–6, USNPC 86383.

Type locality: Bylong Station via Richmond, Qld (20º 15′S 142º 15′E).

Type host: *Onychogalea unguifera* (Gould, 1840).

Site in host: stomach.

Distribution: north-western Qld, northern NT.

Diagnostic features (Figs 12 J, K): Males 7.9–10.5 mm; females 10.3–14.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule much wider than long, symmetrical; anterior margin of buccal capsule straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in posterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 2.01–2.28 mm, tips minutely bifid; ala diminishes gradually towards tip; female tail very short, conical; vagina short, highly convoluted; ovejector J-shaped.

***Cloacina middletoni* Beveridge, 2019**

Cloacina middletoni Beveridge, 2019, in Beveridge et al., 2019, pp. 467–469.

Type data: holotype SAM AHC 48280, allotype SAM AHC 48281, paratype SAM AHC 48282.

Type locality: Mount Trio, WA (34º 21′S 118º 07′E).

Type host: *Notamacropus irma* (Jourdan, 1837).

Site in host: stomach.

Distribution: south-western WA.

Representative DNA sequence data: ITS1, ITS2: MK572550, MK573546.

Diagnostic features (Figs 12 H, I): Males 2.7–5.1 mm; females 4.2–5.5 mm; cervical cuticle inflated to level of oesophago-intestinal junction; cephalic papillae: proximal segment obovate; distal segment ovoid, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule sinuous in lateral views; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 1.77–2.27 mm; ala diminishes gradually towards tip; female tail short, conical; vagina short, straight; ovejector J-shaped.

***Cloacina minor* (Davey & Wood, 1938)**

Macropostrongylus minor Davey & Wood, 1938, pp. 259–261, figs 3–5; Skrjabin et al., 1952, p. 292; Popova, 1958, pp. 263–264, fig. 179.

Cloacina minor: Johnston & Mawson, 1939d, p. 208; Yamaguti, 1961, p. 401; Beveridge, 1998a, pp. 431–433, figs 713–724; Beveridge et al., 1998, p. 486.

Type data: syntypes BMNH 1939.1.10.101–7, QM GL12152.

Type locality: Yabulu, Qld (19º 13′S 146º 36′E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Notamacropus agilis* (Gould, 1842); *Notamacropus parryi* (Bennett, 1835).

Site in host: stomach.

Distribution: eastern Qld, north-eastern NSW.

Diagnostic features (Fig. 12 L): Males 4.6–5.9 mm; females 5.2–6.4 mm; cervical cuticle inflated to level of oesophago-intestinal junction; cephalic papillae: proximal segment cylindrical; distal segment ovoid,

shorter than proximal segment, directed medially; lips absent; 8 leaf-crown elements; buccal capsule wider than long, slightly asymmetrical, with dorsal wall more robust; anterior margin of buccal capsule straight; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring; single dorsal oesophageal denticle present; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray short, internal branchlets elongate; spicules 2.04–2.18 mm; ala diminishes gradually towards tip; female tail conical; vagina short, straight; ovejector J-shaped.

Comments: Although the type host of this species was stated to be *Osphranter robustus*, this species has been found to be primarily parasitic in *N. parryi* with an occasional occurrence in sympatric *N. agilis* (Beveridge et al., 1998).

***Cloacina mundayi* Mawson, 1972**

Cloacina mundayi Mawson, 1972, p. 109, figs 1–7; Munday & Green, 1972, p. 6; Beveridge, 1998a, pp. 433–435, figs 725–734.

Type data: holotype and allotype SAM V1505, paratypes SAM AHC 5195.

Type locality: Tarraleah, Tas. (42° 18′S 146° 26′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Other hosts: *Thylogale billardierii* (Desmarest, 1822).

Site in host: stomach.

Distribution: Tas.

Diagnostic features (Fig. 12 T): Males 3.8–6.2 mm; females 6.9–8.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, slightly asymmetrical, with dorsal wall less robust; anterior margin of buccal capsule slightly sinuous; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring; denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore in region of oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; stem of dorsal ray elongate; external branchlets of dorsal ray short, internal branchlets elongate; spicules 1.00–1.19 mm; ala diminishes gradually towards tip; female tail conical; vagina short, straight; ovejector J-shaped.

***Cloacina nephele* Beveridge, 2002**

Cloacina nephele Beveridge, 2002b, pp. 15–17, figs 75–89.

Type data: holotype SAM AHC 31445, allotype SAM AHC 31446, paratypes SAM AHC 31447, BMNH 2001.4.10.9, USNPC 91137.

Type locality: Usino, Madang, PNG (5° 32′S 145° 23′E).

Type host: *Dorcopsis hageni* Heller, 1897.

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 12 R, S): Males 6.1–7.4 mm; females 6.0–7.9 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment ovoid, asymmetrical; distal segment slender, as long as proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, arched anteriorly; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid at level of nerve ring; dorsal lobes of bursa longer than lateral lobes; stem of dorsal ray elongate; external branchlets of dorsal ray short, internal branchlets longer; spicules 1.96–2.10 mm; ala diminishes gradually towards tip; female tail conical; vagina short, recurrent; ovejector J-shaped.

***Cloacina nike* Beveridge, 1998**

Cloacina nike Beveridge, 1998a, pp. 435–437, figs 735–745; Beveridge et al., 1998, p. 486; Beveridge, 2020, p. 5.

Type data: holotype SAM AHC 26813, allotype SAM AHC 26814, paratypes SAM AHC 26815, BMNH 1996.3.21.9–10, USNPC 86385.

Type locality: Rubyvale, Qld (23° 25′S 147° 42′E).

Type host: *Lagorchestes conspicillatus* Gould, 1842.

Other hosts: *Notamacropus parryi* (Bennett, 1835); *Onychogalea unguifera* (Gould, 1840); *Osphranter antilopinus* (Gould, 1842); *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: north-eastern Qld.

Representative DNA sequence data: ITS1, ITS2: MN864143 (unpublished sequence data, morphological voucher specimen SAM AHC 48751).

Diagnostic features (Fig 12 Q): Males 6.6–9.0 mm; females 6.9–9.9 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus slender, without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external

branchlets of dorsal ray very short, internal branchlets long; spicules 2.57–3.36 mm; female tail conical; vagina short, sinuous; ovejector J-shaped.

Comments: This species occurs primarily in *La. conspicillatus* and *O. unguifera* (Beveridge et al., 1992 as *Cloacina* sp.4) with occasional occurrences in sympatric host species.

***Cloacina niobe* Beveridge, 1998**

Cloacina niobe Beveridge, 1998a, pp. 438–440, figs 746–757.

Type data: holotype SAM AHC 26833, allotype SAM AHC 26834, paratypes SAM AHC 26835, 27552–5, BMNH 1996.3.21.13–14, USNPC 86386.

Type locality: Taree, NSW (31º 54'S 152º 29'E).

Type host: *Notamacropus parma* (Waterhouse, 1846).

Site in host: stomach.

Distribution: eastern NSW.

Diagnostic features (Figs 12 M–P): Males 6.3–10.7 mm; females 7.9–29.8 mm; cervical cuticle not inflated; cephalic papillae: proximal segment doliiform; distal segment conical, tapering, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus slender, very long, without bosses; 7–10 transverse folds in lining of anterior oesophagus; 3 sets of small and 1 set of large denticles at entry to oesophageal bulb; nerve ring in anterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; spicules 3.1–3.6 mm; female tail very short, truncated; vagina elongate, sinuous; ovejector J-shaped.

***Cloacina obtusa* Johnston & Mawson, 1939**

Cloacina obtusa Johnston & Mawson, 1939b, p. 530, figs 46–48; 1940b, p. 97, 1940c, p. 365; Skrjabin et al., 1952, p. 162; Popova, 1960, pp. 31–32, fig. 19; Yamaguti, 1961, p. 401; Beveridge & Arundel, 1979, pp. 72, 74; Arundel et al., 1990, p. 42; Pamment et al., 1994, p. 193; Beveridge, 1998a, pp. 440–442, figs 758–769; Beveridge et al., 1998, p. 486; Chilton et al., 2004, p. 207; Webley et al., 2004, p. 625; Aussavy et al., 2011, pp. 14, 15; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240.

Cloacina vestibulata Johnston & Mawson, 1940b, p. 97, figs 1–2; Popova, 1960, pp. 35–36, fig. 23; Yamaguti, 1961, p. 401.

Type data: syntypes SAM V1565.

Type locality: Coonamble, NSW (30º 57'S 148º 24'E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817).

Site in host: stomach.

Distribution: north-eastern Qld, NSW, Vic, Tas, southern SA, southern WA.

Diagnostic features (Fig. 12 U): Males 9.9–14.7 mm; females 14.7–18.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 2.29–3.52 mm, ala diminishes towards tip; female tail conical; vagina short, straight; ovejector J-shaped.

Comments: *Cloacina obtusa* is extremely common in both species of grey kangaroos (*Mac. fuliginosus* and *Mac. giganteus*) throughout their geographical ranges. An allozyme study by Chilton et al. (2004) failed to find significant genetic differences between populations of nematodes from the two host species.

***Cloacina oweni* Beveridge, 2002**

Cloacina oweni Beveridge, 2002b, pp. 17–19, figs 90–101.

Type data: holotype SAM AHC 31448, allotype SAM AHC 31449, paratypes SAM AHC 31450, BMNH 1998.9.28.1–12.

Type locality: Bula Plain, Bensbach, PNG (9º 08'S 141º 01'E).

Type host: *Notamacropus agilis* (Gould, 1842).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Fig. 13 A): Males 5.5–7.5 mm; females 6.7–9.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, shorter than proximal segment; lips present; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus without bosses and folds; single dorsal denticle at level of nerve ring; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 2.19–2.67 mm, ala diminishes towards tip; female tail very short, conical; vagina short, sinuous; ovejector J-shaped.

***Cloacina papillata* Beveridge, 1979**

Cloacina papillata Beveridge, 1979, pp. 367–369 figs 13–24; Beveridge et al., 1985, p. 378; Beveridge, 1998a, pp. 442–445, figs 770–781; Beveridge et al., 1998, p. 486; Aussavy et al., 2011, p.17; Shuttleworth et al., 2014, p. 263; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 213; Spratt et al., 2017, p. 242.

Type data: holotype SAM V1625, allotype SAM V1626, paratypes SAM V1627–44, SAM AHC 11140.

Type locality: Marlborough, Qld (22º 49'S 149º 53'E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: eastern Qld, eastern NSW, Vic.

Representative DNA sequence data: ITS1, ITS2: KM219863–71, 219905, 219897.

Diagnostic features (Fig. 13 B): Males 5.7–7.3 mm; females 6.9–8.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, sub-symmetrical, anterior margin straight; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending full length; folds and denticles absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in posterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 2.10–3.60 mm, ala diminishes towards tip; female tail short, conical; vagina elongate, prominently recurrent; ovejector J-shaped.

Comments: Genetic studies by Shuttleworth et al. (2014) and Chilton et al. (2017) showed that *C. eos* and *C.papillata* were sister species, but their genetic separation was not clear in the observations presented by Shuttleworth et al. (2014). This species pair, frequently synhospitalic, therefore warrants more intensive molecular examination.

***Cloacina papillatissima* Beveridge, 1998**

Cloacina papillatissima Beveridge, 1998a, pp. 445–447, figs 782–791; Shuttleworth et al., 2014, p. 263; Beveridge, 2016, p. 213.

Type data: holotype SAM AHC 266780, allotype SAM AHC 26781, paratypes SAM AHC 26782, 27565–6, BMNH 1996.3.21.26–27, USNPC 86394.

Type locality: Warrandyte, Vic. (37º 45'S 145º 13'E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: eastern Qld, eastern NSW, Vic.

Representative DNA sequence data: ITS1, ITS2: KM219861–2, 219887.

Diagnostic features (Figs 13 C, D): Males 5.6–6.2 mm; females 7.3–8.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, shorter than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, sub-symmetrical, anterior margin straight; dorsal oesophageal tooth projects into buccal capsule; oesophagus with multiple rows of bosses extending to nerve ring, single row extending full length; folds and denticles absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid immediately posterior to nerve ring; lobes of bursa similar; branchlets of dorsal ray short; spicules 0.86–1.04 mm; female tail short, conical; vagina short, straight; ovejector J-shaped.

***Cloacina papuensis* Beveridge, 2002**

Cloacina papuensis Beveridge, 2002b, pp. 19–21, figs 102–115.

Type data: holotype SAM AHC 31451, allotype SAM AHC 31452, paratypes SAM AHC 31453, BMNH 1998.9.28.13–14.

Type locality: Bula Plain, Bensbach, PNG (9º 08'S 141º 01'E).

Type host: *Notamacropus agilis* (Gould, 1842).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 13 E–G): Males 3.2–5.1 mm; females 5.1–6.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses and folds; single dorsal denticle at level of nerve ring; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 1.84–2.26 mm, ala diminishes towards tip; female tail short, conical; vagina short, sinuous; ovejector J-shaped.

***Cloacina parva* Johnston & Mawson, 1938**

Cloacina parva Johnston & Mawson, 1938, pp. 282–283, figs 67–72; 1940b, p. 97; Skrjabin et al., 1952, p. 162; Popova, 1960, pp. 32–33, fig. 20; Mawson, 1961a, p. 82; Yamaguti, 1961, p. 401; Beveridge, 1998a, pp. 447–450, figs 792–805; Beveridge et al., 1998, p. 486; Bradley et al., 2000, p. 39; Shuttleworth et al., 2016a, p. 247; Beveridge, 2020c, p. 5.

Type data: holotype, allotype SAM V1361.

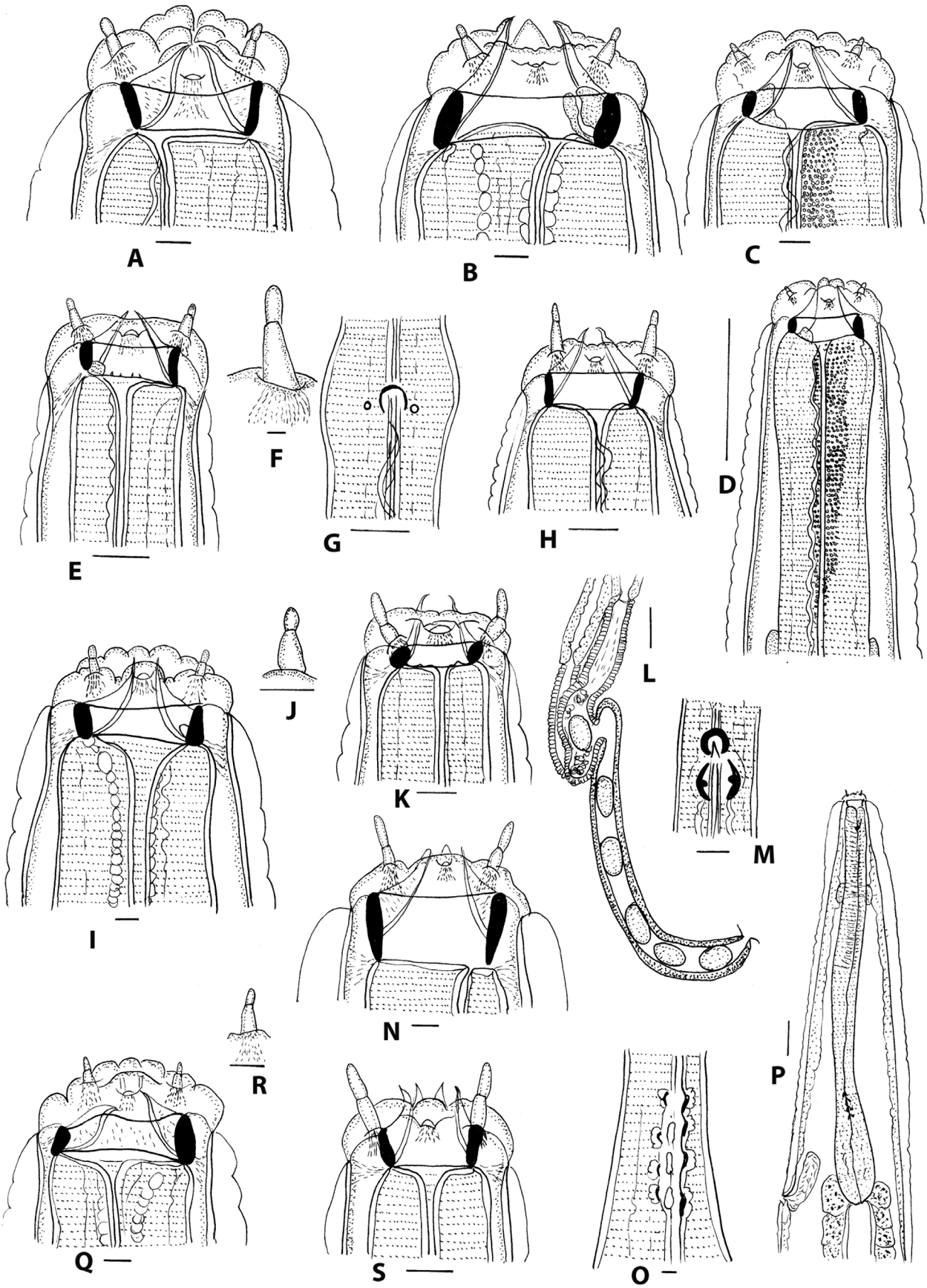
Type locality: Mount Liebig, NT (23° 19'S 131° 22'E).
Type host: *Osphranter robustus* (Gould, 1840).
Other hosts: *Osphranter antilopinus* (Gould 1842); *Petrogale lateralis* Gould, 1840; *Petrogale purpureicollis* Le Souef, 1924; *Petrogale wilkinsi* Thomas, 1926; *Petrogale xanthopus* Gray, 1855 (captive); *Wallabia bicolor* (Desmarest, 1804).
Site in host: stomach.
Distribution: NT, Qld, NSW, SA, WA. Map: Beveridge, 2020c, p. 7.
Representative DNA sequence data: ITS1, ITS2: KU853857–8, 853871, 853873–5, 853877, 853897–99, 853900–02, 853939, 853947, 853954; cox1: KJ851930; 18S, 28S, ITS: KJ776351.
Diagnostic features (Figs 13 I, J, 44 G): Males 8.8–11.9 mm; females 15.6–18.6 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, shorter than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; dorsal oesophageal tooth projects slightly into buccal capsule; oesophagus with bosses extending half way to nerve ring; folds and denticles absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 3.28–5.23 mm, ala diminishes towards tip; female tail short, conical; vagina long, prominently recurrent; ovejector J-shaped.
Comments: Most records of this species are from *O. robustus* with the records from other host species being single collections or from a small number of animals. The record from *Pet. xanthopus* is from a captive population in the Adelaide Zoo, SA. Shuttleworth et al. (2016a) noted considerable genetic variation within *C. parva* with two distinct sub-clades. However, there was no obvious geographical pattern or association with particular sub-species of *O. robustus*.

***Cloacina pearsoni* Mawson, 1971**

Cloacina pearsoni Mawson, 1971, p. 171, figs 5–8; Beveridge et al., 1989, p. 276; Beveridge, 1998a, pp. 450–453, figs 806–819; Bradley et al., 2000, p. 39; Chilton et al., 2009a, p. 3.
Type data: holotype SAM V3348.
Type locality: Pearson Island, SA (33º 58'S 137º 17'E).
Type host: *Petrogale lateralis pearsoni* Thomas, 1922.
Other hosts: *Petrogale assimilis* Ramsay, 1877; *Petrogale coenensis* Eldridge & Close, 1992; *Petrogale godmani* Thomas, 1923; *Petrogale herberti* Thomas, 1926; *Petrogale inornata* Gould, 1842; *Petrogale lateralis* Gould, 1840, MacDonnell Ranges race; *Petrogale mareeba* Eldridge & Close, 1992; *Petrogale penicillata* (Gray, 1827); *Petrogale purpureicollis* Le Souef, 1924; *Petrogale sharmani* Eldridge & Close, 1992; *Petrogale wilkinsi* Thomas. 1926; *Petrogale xanthopus* Gray, 1855.
Site in host: stomach.
Distribution: NT, Qld, NSW, SA.
Representative DNA sequence data: ITS1, ITS2: FM 992599–602, 992604; 18S: KJ776352, 776357–8; cox1: KJ851931–6.
Diagnostic features (Fig. 13 H): Males 4.1–6.0 mm; females 4.8–9.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; dorsal oesophageal tooth projects slightly into buccal capsule; oesophagus without denticles, bosses and folds; nerve ring in mid-oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray variable; spicules 1.10–1.55 mm, tip minutely bifid, ala diminishes towards tip; female tail short, conical; vagina short, straight; ovejector J-shaped.
Comments: This nematode species, which is found in a range of species of rock wallabies (*Petrogale* spp.), is

Fig. 13. Genus *Cloacina*. A, *Cloacina oweni*, buccal capsule, lateral view; B, *Cloacina papillata*, buccal capsule, lateral view; C, *Cloacina papillatissima*, buccal capsule, lateral view; D, *C. papillatissima*, anterior oesophagus, lateral view; E, *Cloacina papuensis*, buccal capsule, lateral view; F, *C. papuensis*, cephalic papilla; G, *C. papuensis*, oesophageal denticles, dorsal view; H, *Cloacina pearsoni*, buccal capsule, lateral view; I, *Cloacina parva*, buccal capsule, lateral view; J, *Cloacina parva*, cephalic papilla; K, *Cloacina pelops*, buccal capsule, lateral view; L, *C. pelops*, vagina, lateral view; M, *C. pelops*, oesophageal denticles, dorsal view; N, *Cloacina petrogale*, buccal capsule, lateral view; O, *C. petrogale*, oesophageal denticles, lateral view; P, *C. petrogale*, oesophagus, lateral view; Q, *Cloacina phaethon*, buccal capsule, lateral view; R, *C. phaethon*, cephalic papilla; S, *Cloacina pollux*, buccal capsule, lateral view. (A, E–G, from Beveridge, 2002b; B–D, H–S from Beveridge, 1998a).

Scale-bars: D, L, P, 0.1 mm; A–C, E–K, M–O, Q–S, 0.01 mm.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highly variable morphologically (Beveridge, 1998a). A genetic study of populations from *Pet. assimilis*, *Pet. herberti*, *Pet. inornata* and *Pet. mareeba* (Chilton et al., 2009a) revealed significant genetic differences between each population, suggesting the existence of a species complex.

***Cloacina pelops* Beveridge, 1998**

Cloacina pelops Beveridge, 1998a, pp. 453–455, figs 682, 820–830; Aussavy et al., 2011, pp. 14, 15: Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 244.

Type data: holotype SAM AHC 27338, allotype SAM AHC 27339, paratypes SAM AHC 10934, 27652–5, BMNH 1996.3.21.35–36, USNPC 86389.

Type locality: Tidbinbilla, ACT (35° 27′S 148° 52′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817).

Site in host: stomach.

Distribution: NSW, ACT, Vic, Tas.

Diagnostic features (Figs 13 K–M): Males 6.6–9.4 mm; females 11.1–14.3 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment doliiform; distal segment ovoid, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus with 3 denticles anterior to nerve ring, dorsal denticle anterior to 2 sub-ventral denticles; bosses and folds absent; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 2.09–2.83 mm; ala diminishes towards tip; female tail short, conical; vagina short, straight; ovejector J-shaped.

Comment: This species is primarily parasitic in *Mac. giganteus* in south-eastern Australia and has been found in one population of *Mac. fuliginosus* in an area of sympatry in Victoria (Aussavy et al., 2011).

***Cloacina petrogale* Johnston & Mawson, 1938**

Cloacina petrogale Johnston & Mawson, 1938, pp. 277–278, figs 42–46; Skrjabin et al., 1952, p. 162; Popova, 1960, pp. 33–34, fig. 21; Yamaguti, 1961, p. 401; Chilton et al., 1997, p. 485; Beveridge, 1998a, pp. 455–458, figs 835, 842, 843, 848; Bradley et al., 2000, p. 39.

Type data: holotype SAM V2876, allotype SAM V2877, paratypes SAM AHC 1846.

Type locality: Mount Liebig, NT (23° 19′S 131° 22′E).

Type host: *Petrogale lateralis* Gould, 1840 (MacDonnell Ranges race).

Other hosts: *Petrogale purpureicollis* LeSouef, 1924; *Petrogale wilkinsi* Thomas, 1926.

Site in host: stomach.

Distribution: NT, north-western Qld.

Representative DNA sequence data: 18S, 28S, ITS: MF284689 KJ776359; cox1: KJ851937.

Diagnostic features (Figs 13 N–P): Males 6.6–14.0 mm; females 14.0–26.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, tapering, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus slender, very long, without bosses; numerous transverse folds in lining of anterior oesophagus; 4–5 sets of denticles at entry to oesophageal bulb; nerve ring in anterior oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; spicules 1.70–2.50 mm; ala diminishes towards tip; gubernaculum, oval; female tail very short, truncated; vagina elongate, sinuous; ovejector J-shaped.

Comments: Prior to 1998, several species were included under this name (Beveridge, 1998a, p. 455). Electrophoretic studies (Chilton et al., 1997) provided initial evidence that *C. petrogale* was a species complex and these conclusions have subsequently been supported by DNA sequence data (Chilton et al., 2017). However, additional species may exist within this complex.

***Cloacina petronius* Beveridge, 1998**

Cloacina petronius Beveridge, 1998a, pp. 459–461, figs 831–834, 836–841, 844, 848.

Type data: holotype SAM AHC 30177, allotype SAM AHC 30178, paratypes SAM AHC 13176, BMNH 1996.3.21.17–90, USNPC 86389.

Type locality: Torver Valley Station via Hughenden, Qld (20° 41′S 144° 08′E).

Type host: *Petrogale assimilis* Ramsay, 1877.

Other hosts: *Petrogale coenensis* Eldridge & Close, 1992; *Petrogale godmani* Thomas, 1923; *Petrogale herberti* Thomas, 1926; *Petrogale inornata* Gould, 1842; *Petrogale mareeba* Eldridge & Close, 1992; *Petrogale sharmani* Eldridge & Close, 1992.

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, ITS2: FM284690.

Diagnostic features: Males 7.5–9.7 mm; females 14.0–20.8 mm; cervical cuticle not inflated; cephalic papillae:

proximal segment cylindrical; distal segment conical, tapering, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus slender, very long, without bosses; numerous transverse folds in lining of anterior oesophagus; 4–5 sets of denticles at entry to oesophageal bulb; nerve ring in anterior oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; spicules 1.71–1.90 mm; ala diminishes towards tip; gubernaculum, trapezoidal; female tail very short, truncated; vagina elongate, sinuous; ovejector J-shaped.

Comments: The DNA sequence data currently delineating this species were based on specimens from *Pet. assimilis* only (Chilton et al., 2017). Molecular data from additional host species may reveal additional diversity within this species.

***Cloacina phaeax* Beveridge, 1998**

Cloacina phaeax Beveridge, 1998a, pp. 461–462, figs 847–848.

Type data: holotype SAM AHC 26783, allotype SAM AHC 26784, paratypes SAM AHC 26785.

Type locality: Gosse, Kangaroo Island, SA (35° 48′S 136° 59′E).

Type host: *Notamacropus eugenii* (Desmarest, 1817).

Site in host: stomach.

Distribution: SA.

Representative DNA sequence data: ITS1, ITS2: FM284691.

Diagnostic features: Males 5.7–12.1 mm; females 12.3–25.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, tapering, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus slender, very long, without bosses; numerous transverse folds in lining of anterior oesophagus; 4–5 sets of denticles at entry to oesophageal bulb; nerve ring in anterior oesophageal region; excretory pore at level of oesophago–intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; spicules 2.13–2.62 mm; ala diminishes in width and terminates anterior to tip; gubernaculum, triangular; female tail very short, truncated; vagina elongate, sinuous; ovejector J-shaped.

***Cloacina phaedra* Beveridge, 1998**

Cloacina phaedra Beveridge, 1998a, pp. 462–463, figs 846, 848; Beveridge et al., 1998, p. 486.

Type data: holotype SAM AHC 26790, allotype SAM AHC 26784, paratypes SAM AHC 26791, BMNH 1996.3.21.19–20, USNPC 86391.

Type locality: Inkerman Station via Home Hill, Qld (19° 44′S 147° 28′E).

Type host: *Notamacropus parryi* (Bennett, 1835).

Other hosts: *Notamacropus agilis* (Gould, 1842).

Site in host: stomach.

Distribution: north-eastern Qld.

Representative DNA sequence data: 18S, 28S, ITS: FM284692–3.

Diagnostic features: Males 8.5–11.7 mm; females 19.0–25.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, tapering, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus slender, very long, without bosses; numerous transverse folds in lining of anterior oesophagus; 4–5 sets of denticles at entry to oesophageal bulb; nerve ring in anterior oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; spicules 1.94–2.60 mm; ala diminishes in width and terminates anterior to tip; spicule tip minutely bifid; gubernaculum, trapezoidal; female tail very short, truncated; vagina elongate, sinuous; ovejector J-shaped.

Comments: This species is a common parasite of *N. parryi* in north–eastern Queensland and occurs at a much lower prevalence in sympatric *N. agilis* (Beveridge et al., 1998a). Sequence data from specimens from these two host species are identical (Chilton et al., 2017).

***Cloacina phaethon* Beveridge, 1998**

Cloacina phaethon Beveridge, 1998a, pp. 464–466, figs 849–861; Beveridge et al., 1998, p. 486; Shuttleworth et al., 2016a, p. 247; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 26786, allotype SAM AHC 26787, paratypes SAM AHC 26788, BMNH 1996.3.21.21–22, USNPC 86392.

Type locality: Spear Creek Station via Port Augusta, SA (32° 34′S 137° 59′E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Osphranter antilopinus* (Gould, 1842); *Petrogale assimilis* Ramsay, 1877; *Petrogale wilkinsi* Thomas, 1926.

Site in host: stomach.

Distribution: Qld, NSW, SA, WA (Kimberley Division), NT (Top End).

Representative DNA sequence data: ITS1, ITS2: KU853833, 853835, 853843, 853833845–7, 853853, 853860–2, 853865–7, 853880, 853882, 853886, 853888–9, 853915, 853925, 853927–31, 853933–36.

Diagnostic features (Fig. 13 R): Males 7.2–9.4 mm; females 10.9–13.6 mm; cervical cuticle not inflated; cephalic papillae: proximal segment conical; distal segment ovoid, shorter than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, asymmetrical, with dorsal wall shorter than ventral wall; anterior margin sinuous; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring; denticles and folds absent; nerve ring in mid-oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 2.73–4.80 mm; ala diminishes towards tip; female tail short, conical; vagina short, convoluted; ovejector J-shaped.

Comments: Shuttleworth et al. (2016a) found considerable genetic variation within this species, with three recognisable clades. However, there was no obvious geographical pattern or association with the subspecies of *O. robustus*.

***Cloacina pollux* Beveridge, 1979**

Cloacina pollux Beveridge, 1979, pp. 374–376, figs 42–50; Beveridge et al., 1985, p. 378; Beveridge, 1998a, pp. 466–468, figs, 862–871; Beveridge et al., 1998, p. 486; Aussavy et al., 2011, p. 17; Shuttleworth et al., 2014, p. 263; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 213; Spratt et al., 2017, p. 292.

Type data: holotype SAM V1654, allotype SAM V1655, paratypes SAM V1656–70.

Type locality: Townsville, Qld (19° 15′S 146° 49′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: eastern Qld, eastern NSW, Vic.

Representative DNA sequence data: ITS1, ITS2: KM219872–3, 219884–6.

Diagnostic features (Fig. 13 S): Males 3.3–4.5 mm; females 4.1–5.5 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; dorsal oesophageal tooth projects slightly into buccal capsule; oesophagus without denticles and folds; 2 rows of sub-ventral bosses extend to deirid; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray variable; spicules 0.82–1.57mm, ala diminishes towards tip; female tail elongate, conical; vagina short, straight; ovejector J-shaped.

***Cloacina polymela* Beveridge, 2002**

Cloacina polymela Beveridge, 2002b, pp. 21–23, figs 116–128; Spratt & Beveridge, 2016, p. 127.

Type data: holotype SAM AHC 31454, allotype SAM AHC 31455, paratypes SAM AHC 31456, BMNH 2001.4.10.10–11, USNPC 91138.

Type locality: Usino, Madang, PNG (5° 32′S 145° 23′E).

Type host: *Dorcopsis hageni* Heller, 1897.

Other hosts: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 14 A, B): Males: 5.9–6.0 mm; females 5.5–8.2 mm; anterior end deviated dorsally; cervical cuticle prominently inflated; cephalic collar projects prominently; cephalic papillae: proximal segment cylindrical; distal segment conical, longer than proximal segment; lips present; 8 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin sinuous; oesophagus wider anteriorly, without bosses, denticles and folds; nerve ring in posterior oesophageal region; excretory pore in posterior oesophageal region; deirid in mid-oesophageal region; dorsal lobe of bursa longer than lateral lobes; external branchlets of dorsal ray short; internal branchlets elongate; spicules 2.61–2.71 mm, ala diminishes towards tip; female tail short, conical; vagina long, sinuous; ovejector J-shaped.

***Cloacina polyxena* Beveridge, 1998**

Cloacina polyxena Beveridge, 1998a, pp. 468–470, figs 827–884; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 26792, allotype SAM AHC 26793, paratypes SAM AHC 26794, 26576–80.

Type locality: Napier Downs Station via Derby, WA (17º 15′S 124º 44′E).

Type host: *Osphranter antilopinus* (Gould, 1842).

Other hosts: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: WA (Kimberley Division); NT (Top End); Map: Beveridge, 2020c, p. 8.

Diagnostic features (Figs 14, C, D): Males 4.3–5.2 mm;

females 5.5–7.2 mm; cervical cuticle not inflated; cephalic papillae: proximal segment ovoid, asymmetrical; distal segment conical, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical in lateral view, arched anteriorly in dorsal view, anterior margin straight; large dorsal oesophageal tooth and 2 subventral teeth project into buccal capsule; oesophagus without folds; bosses extend to nerve ring; single dorsal denticle present; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray short, internal branchlets elongate; spicules 0.69–0.73 mm; female tail short, conical; vagina extremely short; ovejector J-shaped.

***Cloacina polyxo* Beveridge, 1998**

Cloacina polyxo Beveridge, 1998a, pp. 470–472, figs 885–897; Beveridge et al., 1998, p. 486; Turni & Smales, 2001, p. 406.

Type data: holotype SAM AHC 26818, allotype SAM AHC 26819, paratypes SAM AHC 26820, 27583, BMNH 1996.3.21.23–26, USNPC 86393.

Type locality: Warrawee Station via Charters Towers, Qld (20° 18′S 146° 38′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Other hosts: *Onychogalea fraenata* (Gould, 1840).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, ITS2: MF284694.

Diagnostic features (Figs 14 E, F): Males 3.2–3.9 mm; females 3.4–4.3 mm; cervical cuticle inflated; cephalic papillae: proximal segment conical; distal segment cylindrical, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, extremely shallow, asymmetrical in lateral view with ventral wall thicker than dorsal, arched anteriorly in dorsal view, anterior margin sinuous; large dorsal oesophageal tooth and 2 sub-ventral teeth project into buccal capsule; oesophagus without folds and denticles; bosses extend to nerve ring; nerve ring in posterior oesophageal region; excretory pore at oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; dorsal ray elongate, external branchlets of dorsal ray short, internal branchlets longer; spicules 0.69–0.79 mm; female tail conical; vagina short, straight; ovejector J-shaped.

***Cloacina praxithea* Beveridge, 2002**

Cloacina praxithea Beveridge, 2002b, pp. 23–25, figs 129–138.

Type data: holotype SAM AHC 31457, paratypes SAM AHC 31458, BMNH 2001.4.10.12, USNPC 91139.

Type locality: Usino, Madang, PNG (5° 32′S 145° 23′E).

Type host: *Dorcopsis hageni* Heller, 1897.

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Fig. 14 G): Males: 3.7–5.3 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment cylindrical, asymmetrical; distal segment ovoid, shorter than proximal segment; amphids well posterior to cephalic papillae; lips present; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin sinuous; oesophagus sub-cylindrical, without bosses, folds and denticles; nerve ring in posterior oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray short, internal branchlets longer; spicules 1.30–1.58 mm, ala terminates anterior to spicule tip; female unknown.

Comments: This species is unique in having the amphids well posterior to the cephalic papillae.

***Cloacina procris* Beveridge, 2002**

Cloacina procris Beveridge, 2002b, pp. 25–27, figs 139–153; Spratt & Beveridge, 2016, p. 127.

Type data: holotype SAM AHC 31459, allotype SAM AHC 31460, paratypes SAM AHC 31461.

Type locality: Usino, Madang, PNG (5° 32′S 145° 23′E).

Type host: *Dorcopsis hageni* Heller, 1897.

Other hosts: *Dorcopsis muelleri* (Shlegel, 1866).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 14 H, I): Males: 3.3–4.5 mm; females 4.3–5.2 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment cylindrical, asymmetrical; distal segment ovoid, shorter than proximal segment; lips present; 8 leaf-crown elements; buccal capsule wider than long, asymmetrical, arched anteriorly, dorsal wall smaller than ventral wall; anterior margin arched; oesophagus with bosses extending to nerve ring; single dorsal denticle; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid posterior to nerve ring; dorsal lobe of bursa longer than lateral lobes; external branchlets of dorsal ray short, internal branchlets longer; spicules 1.30–1.58 mm, ala terminates anterior to spicule tip; female tail conical; vagina short, straight; ovejector J-shaped.

***Cloacina ridei* Beveridge, 2014**

Cloacina ridei Beveridge, 2014, pp. 250–252, figs 1–13.

Type data: holotype SAM AHC 46968, allotype SAM AHC 46969, paratypes SAM AHC 14557.

Type locality: Wedge Point, Bernier Island, WA (24° 47′S 113° 09′E).

Type host: *Lagostrophus fasciatus* (Péron & Lesueur, 1807).

Site in host: stomach.

Distribution: Bernier and Dorré Islands, WA.

Diagnostic features (Figs 14 J–L): Males: 5.3–7.3 mm; females 8.7–10.7 mm; cervical cuticle inflated in anterior oesophageal region; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much larger than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule much wider than long, symmetrical, anterior margin straight; oesophagus without bosses; three sets of denticles immediately anterior to oesophageal bulb; c 50 folds present in anterior oesophageal region; nerve ring in anterior oesophageal region; excretory pore in anterior oesophageal region; deirid anterior to nerve ring; lobes of bursa similar; externo-lateral ray arises from dorsal trunk; branchlets of dorsal ray short; spicules 3.10–3.40 mm, ala terminates anterior to spicule tip; female tail short, conical; vagina short, slightly sinuous; ovejector J-shaped.

Comments: This species, along with *C. biscoei* from the same host species, shares the unusual features of the externo-dorsal ray arising from the dorsal trunk and an anteriorly placed excretory pore.

***Cloacina robertsi* Johnston & Mawson, 1939**

Cloacina robertsi Johnston & Mawson, 1939a, pp. 129–130, figs 16–19; Yamaguti, 1961, p. 401; Beveridge, 1998a, pp. 472–474, figs 898–921; Chilton et al. 2009a, p. 3.

Type data: holotype SAM V1547.

Type host: *Petrogale herberti* Thomas, 1926 (as *Petrogale penicillata* (Gray, 1827)).

Other hosts: *Petrogale assimilis* Ramsay, 1877; *Petrogale coenensis* Eldridge & Close, 1992; *Petrogale godmani* Thomas, 1923; *Petrogale inornata* Gould, 1842; *Petrogale mareeba* Eldridge & Close, 1992; *Petrogale penicillata* (Gray, 1827); *Petrogale persephone* Maynes, 1982; *Petrogale sharmani* Eldridge & Close, 1992; *Petrogale wilkinsi* Thomas, 1926; *Petrogale xanthopus* Gray, 1855 (captive animal).

Site in host: stomach.

Distribution: eastern Qld, NT (Top End).

Representative DNA sequence data: ITS1, ITS2: FM 992605–11; cox 1 KJ851938–54; 18S KJ776360–76.

Diagnostic features (Figs 14 M, N): Males: 9.3–11.6 mm; females 14.1–16.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin very slightly sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 3.30–3.90 mm; female tail short, conical; vagina elongate, prominently recurrent; ovejector J-shaped.

Comments: Genetic studies by Chilton et al. (2009a) suggest that *C. robertsi* may be a species complex.

***Cloacina sancus* Beveridge & Speare, 1999**

Cloacina sancus Beveridge & Speare, 1999, pp. 88–89, figs 11–23.

Type data: holotype SAM AHC 31194, allotype SAM AHC 31195, paratypes SAM AHC 31196, BMNH 1998.9.29.15.

Type locality: Doido, Chimbu Province, PNG (6° 33′S 144° 50′E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

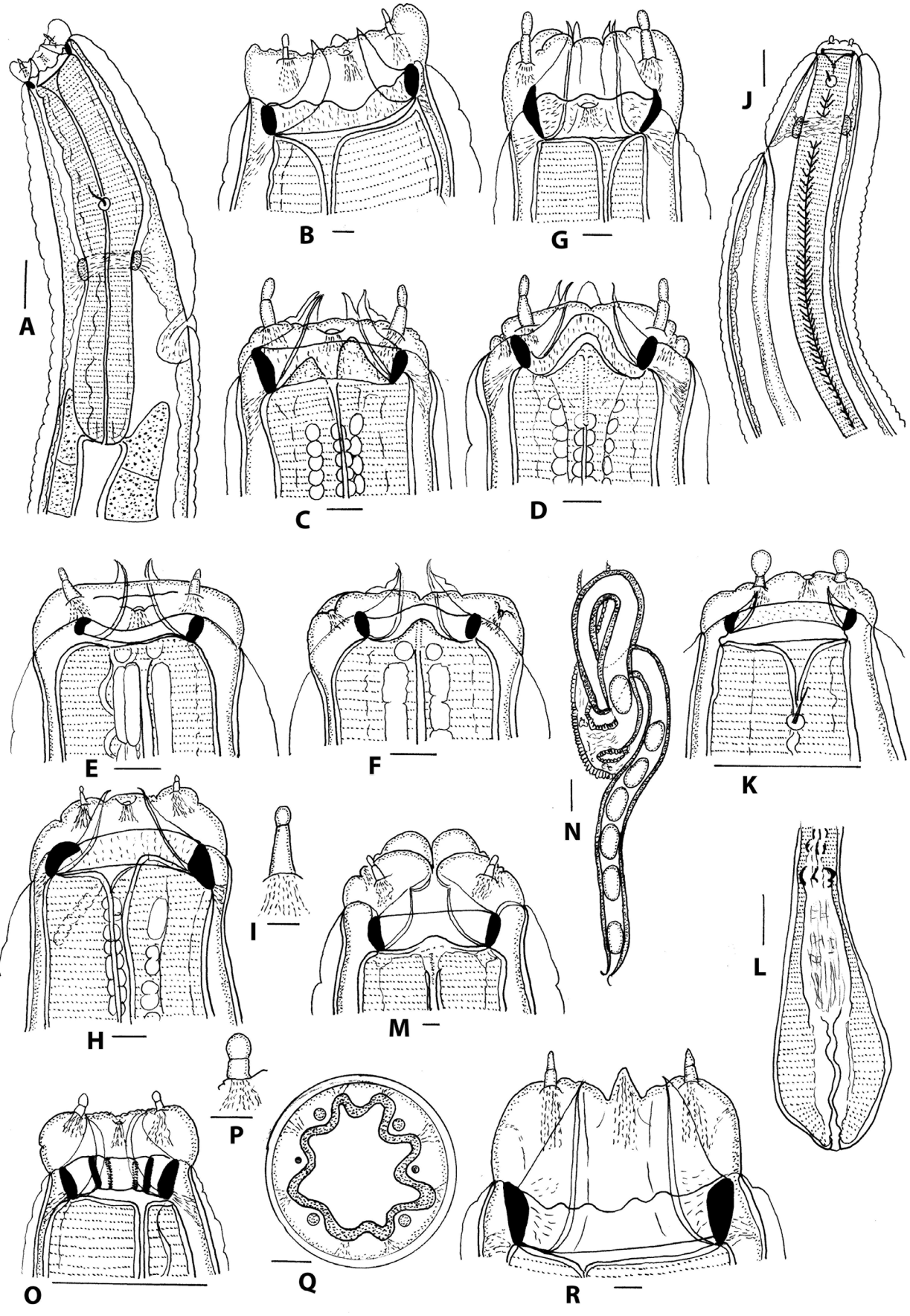
Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 14 O–Q): Males: 4.8–6.6 mm; females 5.5–11.2 mm; cervical cuticle not inflated;

Fig. 14. Genus *Cloacina*. A, *Cloacina polymela*, oesophagus, lateral view; B, *C. polymela*, buccal capsule, lateral view; C, D, *Cloacina polyxena*, C, buccal capsule, lateral view; D, buccal capsule, dorsal view; E, F, *Cloacina polyxo*, E, buccal capsule, lateral view; F, buccal capsule, dorsal view; G, *Cloacina praxithea*, buccal capsule, lateral view; H, *Cloacina procris*, buccal capsule, lateral view; I, *C. procris*, cephalic papilla; J, *Cloacina ridei*, anterior oesophagus, lateral view; K, *C. ridei*, buccal capsule, lateral view; L, *C. ridei*, oesophageal bulb, lateral view; M, *Cloacina robertsi*, buccal capsule, lateral view; N, *C. robertsi*, vagina, lateral view; O, *Cloacina sancus*, buccal capsule, lateral view; P, *C. sancus*, cephalic papilla; Q, *C. sancus*, optical transverse section through buccal capsule; R, *Cloacina sappho*, buccal capsule, lateral view. (A, B, G–I, from Beveridge, 2002b; C–F, M, N, from Beveridge, 1998a; J–L from Beveridge, 2014; O–R, from Beveridge & Speare, 1999).

Scale-bars: A, J–L, N, O, 0.1 mm; B–H, M, P–R, 0.01 mm, I, 0.002 mm.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cephalic papillae: proximal segment short, cylindrical; distal segment ovoid, obtuse as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin very slightly sinuous, highly sinuous in apical views; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray short, internal branchlets elongate; spicules 1.73–2.67 mm; ala terminates anterior to tip; female tail short, conical; vagina elongate, sinuous; ovejector J-shaped.

***Cloacina sappho* Beveridge & Speare, 1999**

Cloacina sappho Beveridge & Speare, 1999, pp. 90, 92–93, figs 35–43.

Type data: holotype SAM AHC 31188, allotype SAM AHC 31189, paratypes SAM AHC 31190.

Type locality: Doido, Chimbu Province, PNG (6° 33'S 144° 50'E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Fig. 14 R): Males: 5.0–6.3 mm; females 5.9–8.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment acute, sub–triangular, longer than proximal segment; amphids on conical projections; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid immediately anterior to nerve ring; lobes of bursa similar; dorsal ray elongate, external branchlets of dorsal ray short, internal branchlets elongate; spicules 1.30–1.50 mm; ala terminates anterior to tip; female tail short, conical; vagina short, straight; ovejector J-shaped.

***Cloacina schultzi* Beveridge, 2019**

Cloacina schultzi Beveridge, 2019, pp. 12–15, figs 33–41.

Type data: holotype SAM AHC 48312, allotype SAM AHC 48313 (incorrectly cited as 38312), paratypes SAM AHC 8175.

Type locality: Moolawatana Station via Lyndhurst, SA (29° 54'S 139° 44'E).

Type host: *Petrogale xanthopus* Gray, 1855.

Site in host: stomach.

Distribution: northern SA.

Diagnostic features (Figs 15 A, B): Males: 5.8–6.8 mm; females 6.4–7.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, very shallow, symmetrical; anterior margin very slightly sinuous or arched; oesophagus subcylindrical, without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray similar; spicules 2.00–2.13 mm; ala diminishes gradually to tip; female tail short, conical; vagina short, recurrent; ovejector J-shaped.

***Cloacina sciron* Beveridge & Speare, 1999**

Cloacina sciron Beveridge & Speare, 1999, pp. 93–95, figs 44–54.

Type data: holotype SAM AHC 31207, allotype SAM AHC 31208, paratypes SAM AHC 31290–10, BMNH 1998.9.28.16–17.

Type locality: Doido, Chimbu Province, PNG (6° 33'S 144° 50'E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

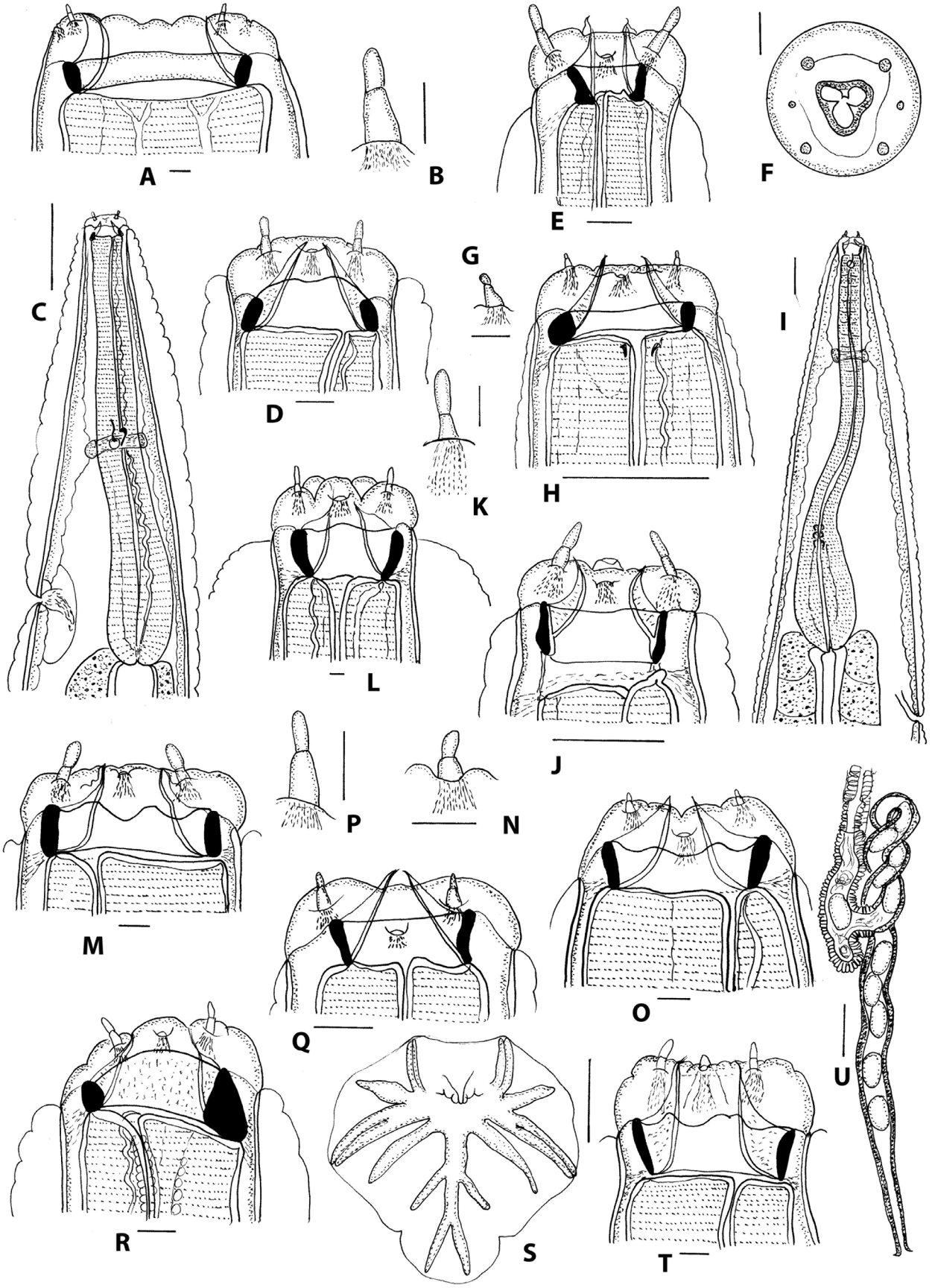
Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 15 C, D): Males: 4.0–6.1 mm; females 3.7–6.8 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal ovoid, as long as proximal segment; lips absent; 8 leaf-crown

Fig. 15. Genus *Cloacina*. A, *Cloacina schultzi*, buccal capsule, lateral view; B, *C. schultzi*, cephalic papilla; C, *Cloacina sciron*, oesophagus, lateral view; D, *C. sciron*, buccal capsule, lateral view; E, *Cloacina selene*, buccal capsule, lateral view; F, *C. selene*, optical transverse section through buccal capsule; G, *Cloacina setonicis*, cephalic papilla; H, *C. setonicis*, buccal capsule, lateral view; I, *Cloacina similis*, oesophagus, lateral view; J, *C. similis*, buccal capsule, lateral view; K, *Cloacina smalesae*, cephalic papilla; L, *C. smalesae*, buccal capsule, lateral view; M, *Cloacina solon*, buccal capsule, lateral view; N, *Cloacina solymus*, cephalic papilla; O, *C. solymus*, buccal capsule, lateral view; P, *Cloacina spearei*, cephalic papilla; Q, *C. spearei*, buccal capsule, lateral view; R, *Cloacina sterope*, buccal capsule, lateral view; S, *Cloacina syphax*, bursa; T, *C. syphax*, buccal capsule, lateral view; U, *C. syphax*, vagina, lateral view. (A, B, from Beveridge, 2019; C, D, M–O, R–U, from Beveridge & Speare, 1999; E–L, from Beveridge, 1998a; P, Q, from Beveridge et al, 2018).

Scalebars: C, H–J, S, U, 0.1 mm; A, B, D–G, K–R, T, 0.01 mm.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elements; buccal capsule wider than long, symmetrical; anterior margin arched anteriorly; oesophagus without bosses and folds; single dorsal denticle; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid at level of nerve ring; lobes of bursa similar; dorsal ray elongate, branchlets of dorsal ray similar; spicules 2.83–3.30 mm, tip recurved; ala diminishes to tip; female tail short, conical; vagina elongate, sinuous; ovejector J-shaped.

***Cloacina selene* Beveridge, 1998**

Cloacina selene Beveridge, 1998a, pp. 476–479, figs 913–924; Webley et al., 2004, p. 625; Aussavy et al., 2011, pp. 14, 15; Schultz et al., 2011, p. 238; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240.

Type data: holotype SAM AHC 26759, allotype SAM AHC 26796, paratypes SAM AHC 26797, BMNH 1996.3.21.30–31, USNPC 86396.

Type locality: Avalon, Vic. (38º 05′S 144º 25′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817); *Petrogale penicillata* (Gray, 1827).

Site in host: stomach.

Distribution: south-eastern NSW, Vic, Tas, southern SA, south-western WA.

Diagnostic features (Figs 15 E, F): Males: 7.2–9.1 mm; females 8.3–9.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal ovoid, as long as proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus slender, without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; dorsal ray variable, external branchlets of dorsal ray slightly or much shorter than internal branchlets; spicules 1.10–1.26 mm; ala diminishes to tip; female tail conical; vagina short, straight; ovejector J-shaped.

Comments: This species is a common parasite of the grey kangaroos, *Mac. fuliginosus* and *Mac. giganteus* (Beveridge, 1998a). The single record from *Pet. penicillata* is from a captive-bred animal released into the wild in Victoria in an area where both species of grey kangaroo are common (Schultz et al., 2011).

***Cloacina setonicis* Mawson, 1961**

Cloacina setonicis Mawson, 1961a, pp. 81–82, figs 1–5; Mawson, 1961b, p. 88, fig. 1; Beveridge, 1998a, pp. 479–481, figs 925–935.

Type data: holotype SAM V2899, allotype SAM V2900, paratypes SAM AHC 4532.

Type locality: Rottnest Island, WA (31º 59′S 115º 31′E).

Type host: *Setonix brachyurus* (Quoy & Gaimard, 1830).

Distribution: south-western WA.

Representative DNA sequence data: ITS1, ITS2: MF284695.

Diagnostic features (Figs 15 G, H): Males: 3.8–7.5 mm; females 4.8–10.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, very shallow, symmetrical; anterior margin slightly sinuous; oesophagus sub-cylindrical, without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid at level of nerve ring; lobes of bursa similar; external branchlets of dorsal ray shorter than internal branchlets; spicules 2.12–2.40 mm; ala diminishes to tip; female tail short, conical; vagina elongate, straight; ovejector J-shaped.

***Cloacina similis* Johnston & Mawson, 1939**

Cloacina similis Johnston & Mawson, 1939a, p. 131, figs 23–24; 1939b, pp. 532–533; Skrjabin et al., 1952, p. 162; Popova, 1960, p. 34; Yamaguti, 1961, p. 401; Beveridge et al., 1989, p. 267; Chilton et al., 1997, p. 485; Beveridge, 1998a, pp. 481–485, figs 936–946; Beveridge et al., 1998, p. 486.

Cloacina clarkae Mawson, 1972, pp. 109, 112, figs 8–13.

Type data: syntypes SAM V1549, SAM AHC 3096.

Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).

Type host: *Petrogale herberti* Thomas, 1926 (as *Petrogale penicillata* (Gray, 1827)).

Other hosts: *Notamacropus dorsalis* (Gray, 1837); *Notamacropus eugenii* (Desmarest, 1817); *Petrogale assimilis* Ramsay, 1877; *Petrogale godmani* Thomas, 1923; *Petrogale inornata* Gould, 1842; *Petrogale lateralis pearsoni* Thomas, 1922; *Petrogale penicillata* (Gray, 1827); *Petrogale xanthopus* Gray, 1855; *Thylogale billardierii* (Desmarest, 1822); *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: eastern Qld, SA, Tas.

Representative DNA sequence data: 18S, 28S, ITS: KJ776377–83, 851982–6; cox1: KJ851955–8.

Diagnostic features (Figs 15, I, J): Males 5.3–9.0 mm; females 8.2–15.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment conical, tapering, longer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical, anterior margin straight; oesophagus slender, very long, without bosses; 7–10 transverse folds in lining of anterior oesophagus; 3 sets of denticles at entry to oesophageal bulb; nerve ring in anterior oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; spicules 2.10–2.30 mm; gubernaculum, triangular; female tail very short; vagina elongate, sinuous; ovejector J-shaped.

Comments: This species occurs in a wide range of hosts but appears to be particularly common in *N. dorsalis* (Beveridge et al., 1998). Beveridge (1998a) noted considerable metric variation within the taxon particularly in spicule lengths. However, electrophoretic data suggest that a single species is involved (Chilton et al., 1997).

***Cloacina smalesae* Mawson, 1975**

Cloacina smalesae Mawson, 1975, p. 39, figs 1–7; Smales & Mawson, 1987a, p. 11; Beveridge, 1998a, pp. 485–487, figs 947–957.

Type data: holotype, allotype SAM V1514.

Type locality: Kangaroo Island, SA (35° 51′S 137° 10′E).

Type host: *Notamacropus eugenii* (Desmarest, 1817).

Site in host: stomach.

Distribution:, SA (Kangaroo Island), south-western WA.

Diagnostic features (Figs 15 K, L): Males: 6.2–9.7 mm; females 10.8–16.8 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, elongate, longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin very slightly sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray short; spicules 3.92–4.21 mm; ala diminishes towards tip; female tail short, conical; vagina elongate, prominently recurrent; ovejector J-shaped.

Comments: Published records for this species are for Kangaroo Island only. However, specimens in SAM AHC (31951) in the same host species from Perup River in the south west of Western Australia indicate its presence in this region as well.

***Cloacina solon* Beveridge & Speare, 1999**

Cloacina solon Beveridge & Speare, 1999, pp. 90–91, figs 24–34.

Type data: holotype SAM AHC 31203, allotype SAM AHC 31204, paratypes SAM AHC 31205, BMNH 1998.9.28.18–19.

Type locality: Doido, Chimbu Province, PNG (6° 33′S 144° 50′E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Fig. 15 M): Males: 4.8–7.6 mm; females 4.7–6.8 mm; cervical cuticle prominently inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, elongate, longer than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray short, internal branchlets elongate; spicules 2.60–2.94 mm; ala diminishes towards tip; female tail short, conical; vagina elongate, prominently recurrent; ovejector J-shaped.

***Cloacina solymus* Beveridge & Speare, 1999**

Cloacina solymus Beveridge & Speare, 1999, pp. 97–99, figs 68–77.

Type data: holotype SAM AHC 31197, allotype SAM AHC 31198.

Type locality: Doido, Chimbu Province, PNG (6° 33′S 144° 50′E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 15 N, O): Males: 7.8–8.6 mm; female 5.0 mm; cervical cuticle not inflated; cephalic papillae tiny: proximal segment cylindrical; distal segment ovoid, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid at level of nerve ring; lobes of bursa similar; external branchlets of dorsal ray short, internal branchlets elongate; spicules 3.67–3.79 mm; ala diminishes abruptly anterior to tip; female tail short, conical; vagina elongate, prominently recurrent; ovejector J-shaped.

***Cloacina spearei* Beveridge, 2018**

Cloacina spearei Beveridge, 2018 in Beveridge et al., 2018, pp. 529–532, figs 1–11; Beveridge, 2020, p. 5.

Type data: holotype SAM AHC 48090, allotype SAM AHC 48091, paratypes SAM AHC 48092.

Type locality: 18 km SW of Katherine, NT (14° 28′S 132° 16′E).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Osphranter antilopinus* (Gould, 1842).

Site in host: stomach.

Distribution: NT (Top End).

Representative DNA sequence data: ITS1, ITS2: MJ105784–5.

Diagnostic features (Figs 15 P, Q): Males 5.8–6.4 mm; females 6.1–9.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin of buccal capsule straight; prominent dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses and folds; single, dorsal denticle; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray short, internal branchlets longer; spicules 2.05–2.60 mm; ala diminished gradually towards tip; female tail conical; vagina covoluted; ovejector J-shaped.

***Cloacina sterope* Beveridge & Speare, 1999**

Cloacina sterope Beveridge & Speare, 1999, pp. 95–97, figs 55–67; Beveridge, 2002b, p. 27.

Type data: holotype SAM AHC 31191, allotype SAM AHC 31192, paratypes SAM AHC 31193, BMNH 1998.9.28.20.

Type locality: Doido, Chimbu Province, PNG (6º 33′S 144º 50′E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

Other hosts: *Dorcopsis hageni* Heller, 1897.

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Fig. 15 R): Males: 3.5–6.0 mm; females 4.2– 5.5 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, asymmetrical, dorsal wall much smaller than ventral wall; anterior margin sinuous; dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses and folds, with single dorsal denticle; nerve ring in mid-oesophageal region; excretory pore at oesophago-intestinal junction; deirid posterior to nerve ring; lobes of bursa similar; branchlets of dorsal ray short; spicules 1.67–2.07 mm; ala diminishes abruptly anterior to tip; female tail short, conical; vagina short, straight; ovejector J-shaped.

***Cloacina syphax* Beveridge & Speare, 1999**

Cloacina syphax Beveridge & Speare, 1999, pp. 86–88, figs 1–10; Beveridge, 2002b, p. 27; Spratt & Beveridge, 2016, p. 127.

Type data: holotype SAM AHC 31191, allotype SAM AHC 31192, paratypes SAM AHC 31193, BMNH 1998.9.28.20.

Type locality: Doido, Chimbu Province, PNG (6º 33′S 144º 50′E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

Other hosts: *Dorcopsis hageni* Heller, 1897; *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 15 S–U): Males: 3.8–5.5 mm; females 4.1– 5.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin sinuous; oesophagus without bosses, folds and denticles; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid immediately anterior to nerve ring; dorsal lobe of bursa longer than lateral lobes; external branchlets of dorsal ray arise anterior to major bifurcation; spicules 2.50–2.93 mm; ala diminishes towards tip; female tail conical; vagina elongate, recurrent region coiled with ascending region; ovejector J-shaped.

Comments: *Cloacina syphax* shares with *C. eurynome* the feature of having the anterior ascending and descending arms of the vagina intertwined.

***Cloacina telemachus* Beveridge, 1999**

Cloacina telemachus Beveridge, 1999b, pp. 26, 28–29, figs 63–72.

Type data: holotype SAM AHC 30570, allotype SAM AHC 30571, paratypes SAM AHC 30572, BMNH 1998.9.28.23.

Type locality: Rottnest Island, WA (31° 59′S 115° 31′E).

Type host: *Setonix brachyurus* (Quoy & Gaimard, 1830).

Site in host: stomach.

Distribution: south-western WA.

Representative DNA sequence data: ITS1, 2: MF284696.
Diagnostic features (Fig. 16 A): Male 7.0 mm; females 5.9–9.4 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment, directed medially; lips absent; 8 leaf-crown elements; buccal capsule shallow, wider than long, symmetrical; anterior margin straight; oesophagus without bosses, folds or denticles; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid immediately posterior to nerve ring; dorsal lobe of bursa no longer than lateral lobes; external branchlets of dorsal ray short, internal branchlets, elongate; spicules 2.33 mm; vagina elongate, straight; ovejector J-shaped.

***Cloacina themis* Beveridge, 1998**

Cloacina themis Beveridge, 1998a, pp. 487–489, figs 958–968; Beveridge et al., 2019, p. 471.
Type data: holotype SAM AHC 30170, allotype SAM AHC 30169.
Type locality: Jandakot, WA (32° 07′S 115° 50′E).
Type host: *Notamacropus irma* (Jourdan, 1837).
Site in host: stomach.
Distribution: south-western WA.
Representative DNA sequence data: ITS1, 2: MK573548, 573544.
Diagnostic features (Figs 16 B, C, 44 H, I): Males 8.0–9.1 mm; females 15.7–21.0 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, longer than proximal segment, directed medially; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight; oesophagus without bosses and folds; 7–8 sets of denticles immediately anterior to bulb region; nerve ring in anterior oesophageal region; excretory pore posterior to oesophago-intestinal junction; deirid immediately anterior to nerve ring; lobes of bursa similar; branchlets of dorsal ray similar; spicules 1.02–1.23 mm; ala diminishes in width to tip; female tail short, conical; vagina short, straight; ovejector J-shaped.

***Cloacina theope* Beveridge, 2002**

Cloacina theope Beveridge, 2002b, pp. 27–29, figs 154–166.
Type data: holotype USNPC 91140, allotype USNPC 91141, paratypes USNPC 91142, SAM AHC 28390.
Type locality: Huon Peninsula, Morobe Province, PNG (6° 25′S 147° 30′E).
Type host: *Dendrolagus matschiei* Forster & Rothschild, 1907.
Other hosts: *Dendrolagus dorianus* Ramsay, 1883.
Site in host: stomach.
Distribution: PNG.
Diagnostic features (Figs 16 D, E): Males 4.7–5.0 mm; females 6.1–6.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight; oesophagus without bosses and folds; single dorsal denticle immediately anterior to nerve ring; nerve ring in mid-oesophageal region; excretory pore at level of oesophago-intestinal junction; deirid immediately anterior to nerve ring; lobes of bursa similar; branchlets of dorsal ray similar; spicules 2.29–2.63 mm; tip minutely bifid; ala diminishes in width to tip; female tail conical; vagina elongate, recurrent; ovejector J-shaped.

***Cloacina thetidis* Johnston & Mawson, 1939**

Cloacina thetidis Johnston & Mawson, 1939b, p. 532, fig. 55; 1940a, pp. 468, 471; Skrjabin et al., 1952, p. 162; Popova, 1960, pp. 34–35, fig. 22; Yamaguti, 1961, p. 401; Beveridge, 1998a, pp. 489–491, figs 969–980; Beveridge et al., 1998, p. 486.
Type data: holotype (female) SAM V4246.
Type locality: New England, NSW.
Type host: *Thylogale thetis* (Lesson, 1827) (probable host misidentification).
Other hosts: *Notamacropus dorsalis* (Gray, 1837).
Site in host: stomach.
Distribution: eastern Qld, north-eastern NSW.
Representative DNA sequence data: ITS1, 2: MF284697.
Diagnostic features (Figs 16 F, G): Males 5.1–6.5 mm; females 6.1–8.9 mm; cervical cuticle not inflated; cephalic papillae: proximal segment short, cylindrical; distal segment ovoid, much longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, very shallow, symmetrical; anterior margin prominently sinuous, sinuous in apical views; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray similar; spicules 0.73–0.81 mm; female tail conical; vagina short, straight; ovejector Y-shaped.
Comments: Early records of this species suggest a wide host range. However, recent collections suggest that the primary host is *N. dorsalis* and Beveridge (1998a) has provided evidence to indicate that the type host nominated in the original description was most probably misidentified.

***Cloacina tyche* Beveridge, 1998**

Cloacina tyche Beveridge, 1998a, pp. 492–494, figs 981–991; Beveridge et al., 1998, p. 486; Beveridge, 2016, p. 214.

Type data: holotype SAM AHC 26801, allotype SAM AHC 26802, paratypes SAM AHC 26803.

Type locality: 15 km N of Marlborough, Qld (22º 49′S 149º 53′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Other hosts: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, 2: MF284698.

Diagnostic features (Figs 16 H, I): Males 4.2–8.0 mm; females 7.1–10.7 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, much shorterer than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, shallow, symmetrical; anterior margin sinuous; buccal capsule wall with numerous fleck-like punctations on internal surface; dorsal oesophageal tooth projects prominently into buccal capsule; oesophagus without bosses and folds; single set of denticles at level of nerve ring with paired subventral denticles anterior to dorsal denticle; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray similar; spicules 1.89–2.90 mm; female tail conical; vagina short, sinuous; ovejector J-shaped.

Comments: Data available suggest that this species is primarily parasitic in *N. dorsalis* with a single occurrence in a sympatric *Wal. bicolor* (Beveridge et al., 1998).

***Cloacina typhon* Beveridge, 1998**

Cloacina typhon Beveridge, 1998a, pp. 494–496, figs 992–1001; Beveridge et al., 1998, p. 486; Spratt et al., 2017, p. 240; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 26798, allotype SAM AHC 26799, paratypes SAM AHC 26800.

Type locality: Killarny, Qld (28º 20′S 152º 18′E).

Type host: *Macropus giganteus* Shaw,1790.

Other hosts: *Lagorchestes conspicillatus* Gould, 1842; *Notamacropus agilis* (Gould, 1842); *Notamacropus dorsalis* (Gray, 1837); *Notamacropus parryi* (Bennett, 1835); *Osphranter antilopinus* (Gould, 1842; *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: Qld, NSW, Vic, WA (Kimberley Division).

Representative DNA sequence data: ITS1, 2: KU853836, 853913.

Diagnostic features (Fig. 16 J): Males 5.9–7.4 mm; females 6.4–8.1 mm; cervical cuticle slightly inflated; cephalic papillae: proximal segment bulbous; distal segment conical, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, shallow, symmetrical; anterior margin straight; dorsal oesophageal tooth and 2 small sub-ventral teeth project into buccal capsule; oesophagus without denticles, bosses and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa slightly longer than lateral lobes; branchlets of dorsal ray similar; external branchlets extend laterally; spicules 1.30–1.48 mm; female tail conical; vagina short, straight; ovejector J-shaped.

Comments: *Cloacina typhon* appears to be parasitic primarily in *Mac. giganteus* along the east coast of Australia. Its occurrence in other hosts in Queensland is in areas of host sympatry with *Mac. giganteus* (Beveridge et al., 1998). The single record from *O. antilopinus* in Western Australia requires confirmation.

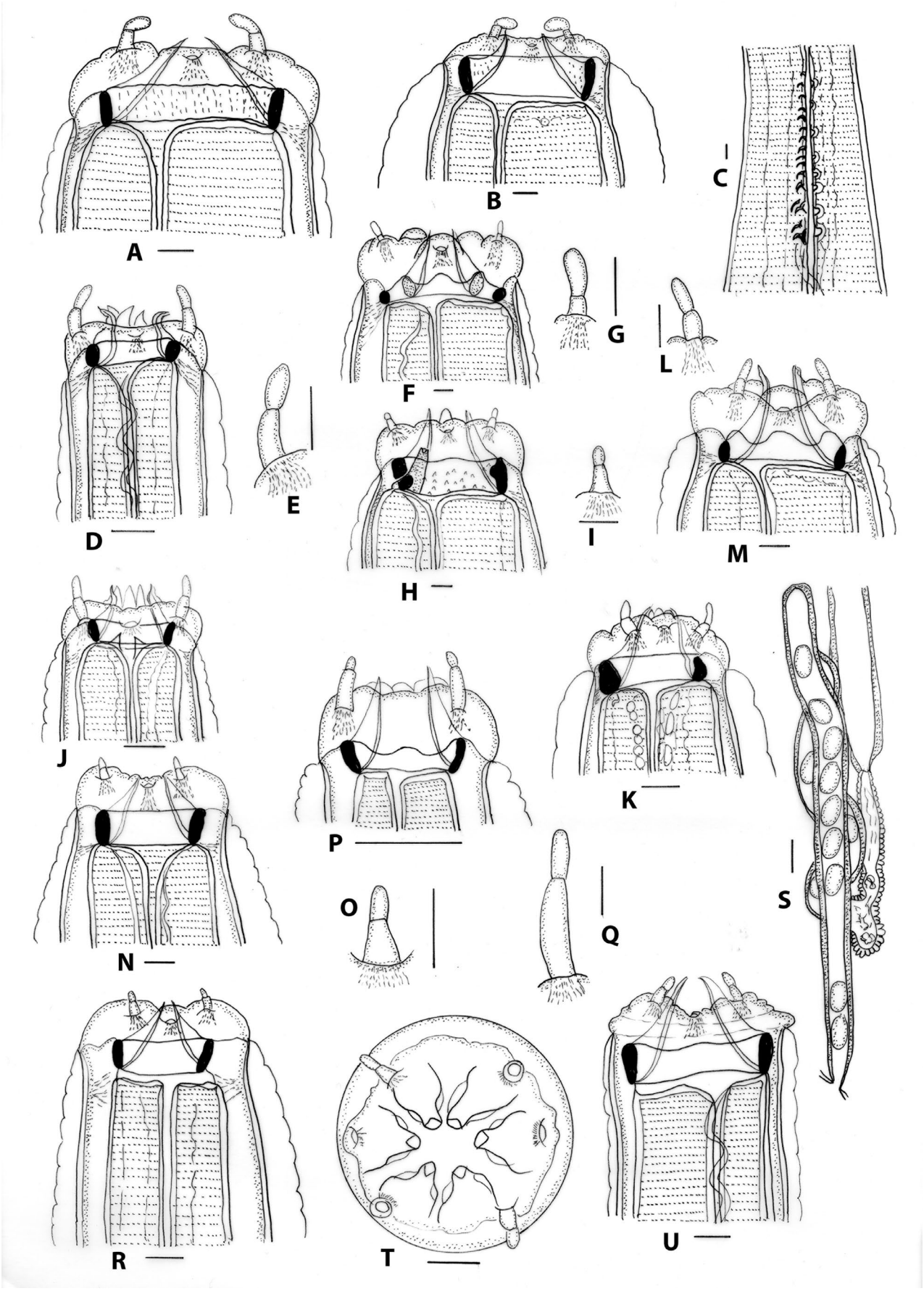
***Cloacina tyro* Beveridge, 1998**

Cloacina tyro Beveridge, 1998a, pp. 496–499, figs 1002–1015; Beveridge et al., 1998, p. 486; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 27340, allotype SAM AHC 27341, paratypes SAM AHC 27342.

Fig. 16. Genus *Cloacina*. A, *Cloacina telemachus*, buccal capsule, lateral view; B, *Cloacina themis*, buccal capsule, lateral view; C, *C. themis*, oesophageal denticles, lateral view; D, *Cloacina theope*, buccal capsule, lateral view; E, *C. theope*, cephalic papilla; F, *Cloacina thetidis*, buccal capsule, lateral view; G, *C. thetidis*, cephalic papilla; H, *Cloacina tyche*, buccal capsule, lateral view; I, *C. tyche*, cephalic papilla; J, *Cloacina typhon*, buccal capsule, lateral view; K, *Cloacina tyro*, buccal capsule, lateral view; L, *Cloacina wallabiae*, cephalic papilla; M, *C. wallabiae*, buccal capsule, lateral view; N, *Cloacina woodi*, buccal capsule, lateral view; O, *C. woodi*, cephalic papilla; P, *Cloacina woworae*, buccal capsule, lateral view; Q, *C. woworae*, cephalic papilla; R, *Cloacina xericola*, buccal capsule, lateral view; S, *C. xericola*, vagina, lateral view; T, *Cloacina zetes*, mouth opening, apical view; U, *C. zetes*, buccal capsule, lateral view. (A–C, F–M, from Beveridge, 1998a; D, E, from Beveridge, 2002b; N, O from Beveridge et al., 2019; P, Q, from Dewi & Purwaningsih, 2020; R, S, from Beveridge, 2018; T, U, from Beveridge, 2019).

Scale-bars: S, 0.1 mm; A–R, T, U, 0.01 mm.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Type locality: 10 km N of Katherine, NT (14° 28′S 132° 16′E).
Type host: *Osphranter robustus* (Gould, 1840).
Site in host: stomach.
Distribution: NT (Top End). Map: Beveridge, 2020c, p. 8.
Diagnostic features (Fig. 16 K): Males 5.6–6.2 mm; females 6.5–7.5 mm; cervical cuticle slightly inflated; cephalic papillae curved medially: proximal segment slightly bulbous; distal segment cylindrical, as long as proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, shallow, asymmetrical, dorsal wall shorter than ventral wall; anterior margin straight; dorsal oesophageal tooth projects into buccal capsule; oesophagus with bosses extending to nerve ring; single dorsal denticle; folds absent; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa slightly longer than lateral lobes; branchlets of dorsal ray similar; spicules 2.02–2.31 mm; female tail conical; vagina sinuous; ovejector J-shaped.

***Cloacina wallabiae* Johnston & Mawson, 1939**

Cloacina wallabiae Johnston & Mawson, 1939b, p. 532, figs 53–53; Skrjabin et al., 1952, p. 162; Popova, 1960, pp. 36–37, fig. 24; Yamaguti, 1961, p. 401; Beveridge, 1979, p. 346; Beveridge et al., 1985, p. 378; Beveridge, 1998a, pp. 499–501, figs 1016–1028; Beveridge et al., 1998, p. 486; Aussavy et al., 2011, p.17; Shuttleworth et al., 2014, p. 263; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 213; Spratt et al., 2017, p. 242.
Type locality: Lower Hawkesbury, NSW (33° 30′S 151° 10′E).
Type data: holotype, allotype SAM V1567.
Type host: *Wallabia bicolor* (Desmarest, 1804).
Other hosts: *Notamacropus parryi* (Bennett, 1835).
Site in host: stomach.
Disytibution: eastern Qld, NSW, Vic.
Representative DNA sequence data: ITS1, 2: KM219874–83, 219888–96.
Diagnostic features (Figs 16 L, M): Males 4.3–7.7 mm; females 6.0–8.9 mm; cervical cuticle not inflated; cephalic papillae directed slightly medially: proximal segment cylindrical; distal segment ovoid, elongate, longer than proximal segment; lips present; 6 leaf-crown elements; buccal capsule wider than long, shallow, symmetrical; anterior margin highly sinuous; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray approximately similar, external branchlets slightly shorter than internals; spicules 1.59–2.31 mm; female tail slender, conical; vagina short, straight; ovejector J-shaped.
Comments: This nematode is a common parasite of *Wal. bicolor* throughout its geographical range. There is only a single record from *N. parryi* from a zone of sympatry with *W. bicolor*.

***Cloacina woodi* Beveridge, 2019**

Cloacina woodi Beveridge, 2019 in Beveridge et al., 2019, pp. 469–471.
Type data: holotype SAM AHC 48287, allotype SAM AHC 48288, paratype SAM AHC 48289.
Type locality: 80 km N of Williams, WA (33° 02′S 116° 53′E).
Type host: *Notamacropus irma* (Jourdan, 1837).
Site in host: stomach.
Distribution: south-western WA.
Diagnostic features (Figs 16 N, O): Male 5.5 mm; females 7.7–8.2 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in posterior oesophageal region; lobes of bursa similar; branchlets of dorsal ray similar; spicules 1.20 mm; ala diminishes in width to tip; female tail conical; vagina short, straight; ovejector J-shaped.

***Cloacina woworae* Dewi & Purwaningsih, 2020**

Cloacina woworae Dewi & Purwaningsih, 2020, pp. 536–537, figs 1A–1, 2A–B.
Type data: holotype, allotype MZB Na 825, paratypes MZB Na 826.
Type locality: Salawati Island, Western New Guinea (1° 06′S 130° 51′E).
Type host: *Dorcopsis muelleri* (Shlegel, 1866).
Site in host: stomach.
Distribution: Western New Guinea.
Diagnostic features (Figs 16 P, Q): Males 4.6–5.3 mm; females 5.5–6.7 mm; cervical cuticle inflated; cephalic papillae: proximal segment cylindrical; distal segment ovoid, shorter than proximal segment; lips absent; 8 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin sinuous; oesophagus broadest immendiately anterior to nerve ring, without bosses, denticles and folds; nerve ring in

mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray shorter than internals; spicules 2.19–2.41 mm; tip obtuse; ala diminishes anterior to tip; female tail conical; vagina very long, slightly sinuous; ovejector J-shaped.

***Cloacina xericola* Beveridge, 2018**

Cloacina xericola Beveridge, 2018, pp. 197–200, figs 1–10; 2020e, p. 240.

Type data: holotype SAM AHC 48129, allotype SAM AHC 48130, paratypes SAM AHC 48131.

Type locality: Menzies, WA (29º 42′S 121º 02′E).

Type host: *Osphranter rufus* (Desmarest, 1822).

Site in host: stomach.

Distribution: central WA. Map: Beveridge, 2018, p. 205.

Diagnostic features (Figs 16 R, S): Males 10.0–13.2 mm; females 15.1–18.1 mm; cervical cuticle not inflated; cephalic papillae: proximal segment cylindrical to conical; distal segment ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements; buccal capsule wider than long, symmetrical; anterior margin straight; dorsal oesophageal tooth projects into buccal capsule; oesophagus without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray shorter than internals; spicules 3.70–5.36 mm; tip minutely bifid; ala diminishes in width abruptly at tip; female tail conical; vagina very long, recurrent, descending arm sinuous; ovejector J-shaped.

***Cloacina zetes* Beveridge, 2019**

Cloacina zetes Beveridge, 2019, pp. 15–18, figs 42–52.

Type data: holotype SAM AHC 48308, allotype SAM AHC 48309, paratypes SAM AHC 48310.

Type locality: Perup River, WA (13º 20′S 116º 27′E).

Type host: *Notamacropus eugenii* (Desmarest, 1817).

Site in host: stomach.

Distribution: south-western WA.

Diagnostic features (Figs 16 T, U): Males 3.8–4.2 mm; females 4.2–4.8 mm; cervical cuticle not inflated; cephalic papillae: proximal segment doliiform; distal segment elongate, ovoid, shorter than proximal segment; lips absent; 6 leaf-crown elements, prominently sculptured in apical view; buccal capsule wider than long, symmetrical; anterior margin straight or very slightly sinuous; oesophagus slender without bosses, denticles and folds; nerve ring in mid-oesophageal region; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; lobes of bursa similar; external branchlets of dorsal ray shorter than internals; spicules 1.50–1.70 mm; tip curved, pointed; ala diminishes gradually in width; female tail conical; vagina short, sinuous; ovejector J-shaped.

Corollonema Beveridge & Chilton, 1998

Type species: *Corol. thylogale* Beveridge & Chilton, 1998.

Generic diagnosis: Cephalic collar present; cephalic papillae domed, armed with single seta; mouth opening circular; external leaf crown of 8 elements; buccal capsule cylindrical, wider than long, heavily sclerotized in posterior region, lacking transverse striations; oesophagus short, with sclerotized annulus at anterior end; terminal bulb ovoid, without sclerotized plates; nerve ring surrounds oesophageal isthmus; excretory pore at level of nerve ring; deirids in anterior oesophageal region; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum poorly sclerotised; ovejector J-shaped.

Comments: This monotypic genus from pademelons (*Thylogale* spp.) is readily recognisable by the prominent leaf crown and the sclerotized annulus at the anterior extremity of the oesophagus.

***Corollonema thylogale* Beveridge & Chilton, 1998**

Corollonema thylogale Beveridge & Chilton, 1998, pp. 159–164, figs 1–17; Griffith et al., 2000, p. 310.

Type data: holotype SAM 30573, allotype SAM 30574, paratypes SAM 30375, BMNH 1997.7.21.1–2, USNPC 87304.

Type locality: Lamington National Park, Qld (28° 12′S 153° 05′E).

Type host: *Thylogale thetis* (Lesson, 1827).

Other hosts: *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: eastern Qld.

Diagnostic features (Figs 17 E–H): Males 5.0–6.5 mm; females 6.2–7.3 mm; spicules 1.55–1.95 mm; vagina elongate, 0.80–0.91 mm; ovejector J– shaped.

Coronostrongylus Johnston & Mawson, 1939

Type species: *Co. coronatus* Johnston & Mawson, 1939.

Other species: *Co. barkeri* Beveridge, 2002; *Co. closei* Beveridge, 2002; *Co. hasegawai* Purwaningsih, Dewi & Smales, 2019; *Co. johnsoni* Beveridge, 2002; *Co. sharmani* Beveridge, 2002; *Co. spearei* Beveridge, 2002; *Co. spratti* Beveridge, 2002.

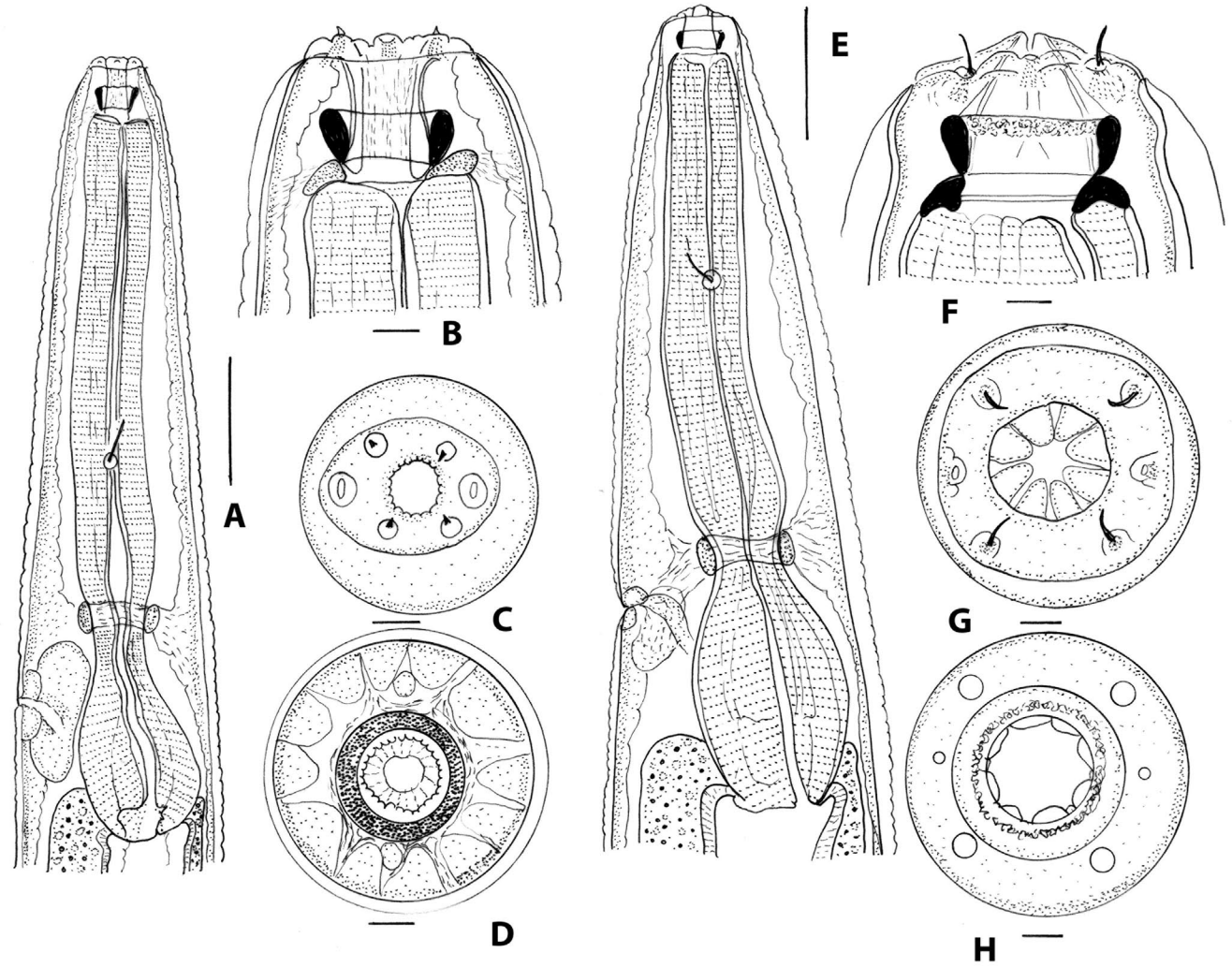


Fig. 17. Genera *Coronostrongylus* and *Corollonema*. A, *Coronostrongylus coronatus*, anterior end, lateral view; B, *Co. coronatus,* buccal capsule, lateral view; C, *Co. coronatus,* buccal anterior end, apical view; D, *Co. coronatus,* optical transverse section through buccal capsule at level of sclerotized ring; E, *Corollonema thylogale*, anterior end, lateral view; F, *Corol. thylogale,* buccal capsule, lateral view; G, *Corol. thylogale,* anterior end, apical view; H, *Corol. thylogale,* optical transverse section through buccal capsule at level of anterior margin of buccal capsule. (Figs A–D from Beveridge, 2002a; E–H from Beveridge & Chilton, 1998).

Scale-bars: A, E, 0.1 mm; B–D, F–H, 0.01 mm.

Generic diagnosis: Cephalic collar present; cephalic papillae domed, each with single seta; mouth opening circular; teeth and leaf crown lacking; buccal capsule with inner, almost transparent wall, folded longitudinally with pleats; base of buccal capsule surrounded by highly sclerotized annulus; oesophagus short, corpus cylindrical, bulb pyriform, without sclerotized plates; nerve ring surrounds oesophageal isthmus; excretory pore at level of nerve ring; deirid in mid or posterior region of oesophagus; bursa with sclerotized bosses; spicules elongate, alate; gubernaculum present; ovejector J-shaped.

Comments: Species of *Coronostrongylus* are readily recognisable in having only the posterior region of the buccal sclerotized and having longitudinal pleats in the anterior region. The species are differentiated primarily on metric characters and therefore the only figures provided are of the generic characters.

Key to species of Coronostrongylus

(separate keys to males and females are given in Beveridge (2002a, pp. 894–895).

1a. Buccal capsule wider than long, externo-dorsal ray fused with postero-lateral ray at base . *Co. spearei*
1b. Buccal capsule longer than wide, externo-dorsal ray arising between postero-lateral and dorsal rays . 2

2a. 24 longitudinal pleats in buccal capsule . . . . . *Co. hasegawai*
2b. >30 longitudinal pleats in buccal capsule 3

3a. 54 longitudinal pleats in buccal capsule, spicules > 1.45 mm . . . . . *C. barkeri*
3b. < 50 longitudinal pleats in buccal capsule, spicules <1.40 mm 4

4a. 46–48 longitudinal pleats in buccal capsule . . . . . *Co. coronatus*
4b. ≤ 40 longitudinal pleats in buccal capsule 5

5a. 40 longitudinal pleats in buccal capsule *Co. spratti*
5b. < 35 longitudinal pleats in buccal capsule 6

6a. 26–30 longitudinal pleats in buccal capsule, spicules 0.69–0.84 (0.76) mm . . . . *Co. johnsoni*
6b. 30–32 longitudinal pleats in buccal capsule, spicules 0.82–1.27 (1.06 mm) 7

7a. 32 longitudinal pleats in buccal capsule, female tail 0.30–0.40 mm . . . . . *Co. closei*
7b. 30 longitudinal pleats in buccal capsule, female tail 0.22–0.28 mm . . . . . *Co. sharmani*

***Coronostrongylus barkeri* Beveridge, 2002**

Coronostrongylus barkeri Beveridge, 2002a, pp. 900–903, figs 11–21; Beveridge, 2002c, p.6; 2002e, p. 204.
Type data: holotype SAM AHC 31490, allotype SAM AHC 31491, paratypes SAM AHC 31492, BMNH 2002.2.18.4–5, USNPC 91775.
Type locality: Bukulla Station via Weilmoringle, NSW (29°14′S 146°55′E).
Type host: *Osphranter rufus* (Desmarest, 1822).
Other hosts: *Onychogalea unguifera* (Gould1840); *Osphranter robustus* (Gould, 1840); *Petrogale wilkinsi* Thomas, 1926 (as *Petrogale brachyotis* (Gould, 1841)).
Site in host: stomach.
Distribution: NT (Arnhem Land), Qld, western NSW. Map: Beveridge, 2002a, p. 902.
Representative DNA sequence data: ITS1, 2: MG865620.
Diagnostic features: Males: 4.4–6.6 mm; females 5.8–8.1 mm; buccal capsule longer than wide; c. 54 longitudinal pleats in buccal capsule; deirid immediately anterior to nerve ring; spicules 1.47–1.87 mm; externo-dorsal ray arises between postero-lateral and dorsal rays; female tail 0.39–0.54 mm; ovejector J-shaped.

***Coronostrongylus closei* Beveridge, 2002**

Coronostrongylus closei Beveridge, 2002a, 903–905, figs 23–31; Beveridge et al., 1989, p. 277 (as *Co. coronatus*); Begg et al., 1995, p. 47 (as *Co. coronatus*).
Type data: holotype SAM AHC 31493, allotype SAM AHC 31494, paratypes SAM AHC 10975, 31495, BMNH 2002.2.18.6–7, USNPC 91776, ANWC N349.
Type locality: Proserpine, Qld (20°24′ S 148°34′E).
Type host: *Petrogale persephone* Maynes, 1982.
Site in host: stomach.
Distribution: Proserpine, Qld.
Representative DNA sequence data: ITS1, 2: MG865621.
Diagnostic features: Males: 3.6–4.7 mm; females 4.4–5.5 mm; buccal capsule longer than wide; c. 32 longitudinal pleats in buccal capsule; deirid in middle of oesophageal corpus; spicules 0.91–1.02 mm; externo-dorsal ray arises between postero-lateral and dorsal rays; female tail 0.30–0.40 mm; ovejector J-shaped.

***Coronostrongylus coronatus* Johnston & Mawson, 1939**

Coronostrongylus coronatus Johnston & Mawson, 1939a, p. 145, fig. 69; 1940a, p. 471, figs 14–17; Popova, 1960, pp. 218–219, fig. 141; Skrjabin et al., 1952, p. 294; Yamaguti, 1961, p. 382; Mawson, 1965, p. 160, figs 59–64; Beveridge et al., 1989, p. 277, 1998, p. 483; Beveridge, 2002a, 895–897, 900, figs 1–10, 72; Aussavy et al., 2011, p. 16; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 245.
Type data: holotype SAM V1560.
Type locality: Eidsvold, Qld (25°22′ S 151°07′E).
Type host: *Thylogale thetis* (Lesson, 1827).
Other hosts: *Notamacropus rufogriseus* (Desmarest, 1817); *Notamacropus dorsalis* (Gray, 1837); *Notamacropus parryi* (Bennett, 1835); *Petrogale inornata* Gould, 1842.
Site in host: stomach.
Distribution: eastern Qld, eastern NSW, Tas. Map: Beveridge, 2002a, p. 897.
Representative DNA sequence data: ITS1, 2: MG865622–3.
Diagnostic features (Figs 17 A–D, 45 A): Males: 4.6–6.1 mm; females 5.5–6.8 mm; buccal capsule longer than wide; 46–48 longitudinal pleats in buccal capsule; deirid posterior to middle of oesophageal corpus;

spicules 1.07–1.37 mm; externo-dorsal ray arises between postero-lateral and dorsal rays; female tail 0.37–0.57 mm; ovejector J-shaped.

Comments: Although Johnston & Mawson (1939a) described this species from *Thyl. thetis*, it has not been found in this host since (Griffith et al., 2000), but is particularly common in *N. rufogriseus* (Beveridge, 2002a; Aussavy et al., 2011; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017). The common names of these hosts (red–necked pademelon and red–necked wallaby) have caused confusion in host identification in the past and the type host may have been misidentified. *Notamacropus dorsalis* and *N. parryi* are uncommon hosts of *Co. coronatus* and are found only where these wallabies are sympatric with *N. rufogriseus* (Beveridge, 2002a). Material from *P. inornata* from Whitsunday Island, Qld, was assigned to this species even though there were minor morphological differences; it may represent a distinct species (Beveridge, 2002a). Johnston & Mawson (1939a) also reported the nematode from *Thyl. stigmatica* (=*T. wilcoxi*), but their specimen is no longer extant and may have been *Co. johnsoni* (see Beveridge, 2002a).

***Coronostrongylus hasegawai* Purwaningsih, Dewi & Smales, 2019**

Coronostrongylus hasegawai Purwaningsih, Dewi & Smales, 2019, pp. 434–437, figs 11–15.

Type data: holotype, allotype MZB Na762, paratypes MZB Na763.

Type locality: Kumawa Mountains, Western New Guinea (1º 6′S 130º 51′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea .

Diagnostic features: Males: 6.1–7.4 mm; females 7.8–8.9 mm; buccal capsule longer than wide; 24 longitudinal pleats in buccal capsule; deirid in posterior part of oesophageal corpus; spicules 0.99–1.16 mm; externo-dorsal ray arises between postero-lateral and dorsal rays; female tail 0.50–0.57 mm; ovejector J-shaped.

***Coronostrongylus johnsoni* Beveridge, 2002**

Coronostrongylus johnsoni Beveridge, 2002a, pp. 905–908, figs 32–42.

Coronostrongylus coronatus pro parte: Beveridge et al., 1989, p. 277, 1992, p. 364, 1998, p.48.

Type data: holotype SAM AHC 31487, allotype SAM AHC 31488, paratypes SAM AHC 8184, BMNH 2002.2.18.3–4, USNPC 91774.

Type locality: Mount Surprise, Qld (18°09′S 144°19′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Other hosts: *Notamacropus rufogriseus* (Desmarest, 1817); *Notamacropus parma* (Waterhouse, 1846); *Petrogale godmani* Thomas, 1923; *Petrogale brachyotis* (Gould, 1841); *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: NT (Arnhem Land), eastern Qld, eastern NSW. Map: Beveridge, 2002a, p. 908.

Representative DNA sequence data: ITS1, 2: MG865624.

Diagnostic features: Males: 3.6–4.7 mm; females 4.2–6.0 mm; buccal capsule longer than wide; 26–30 longitudinal pleats in buccal capsule; deirid in middle of oesophageal corpus; spicules 0.69–0.84 mm; externo-dorsal ray arises between postero-lateral and dorsal rays; female tail 0.23–0.40 mm; ovejector J-shaped.

Comments: The most frequent host of this nematode is *N. dorsalis* although small numbers have been found in *N. rufogriseus* in areas of host sympatry (unpublished data). The material from *N. parma* is extremely fragmentary and requires confirmation. Its presence in *Thyl. stigmatica* may explain the record (as *Co. coronatus*) in this host species by Johnston & Mawson (1939a). The occurrence of the nematode in the Northern Territory is beyond the geographical range of *N. dorsalis*. Beveridge (2002a) noted the disjunct occurrence of *Co. johnsoni* in the Northern Territory, a situation warranting additional investigation.

***Coronostrongylus sharmani* Beveridge, 2002**

Coronostrongylus sharmani Beveridge, 2002a, 908–909, figs 43–52.

Coronostrongylus coronatus pro parte: Beveridge et al., 1989, p. 277.

Type data: holotype SAM AHC 31496, allotype SAM AHC 31497, paratypes SAM AHC 13062, BMNH 2002.2.18.8–9, USNPC 91777.

Type locality: Brooklyn Station via Mareeba, Qld (16°35′S 145°11′E).

Type host: *Petrogale godmani* Thomas, 1923.

Other hosts: *Petrogale coenensis* Eldridge & Close, 1992; *Petrogale mareeba* Eldridge & Close, 1992.

Site in host: stomach.

Distribution: north-eastern Qld. Map: Beveridge, 2002a, p. 911.

Diagnostic features: Males: 3.8–4.8 mm; females 4.8–5.2 mm; buccal capsule longer than wide; c. 30 longitudinal pleats in buccal capsule; deirid in middle of oesophageal corpus; spicules 0.82–1.27 mm; externo-dorsal ray arises between postero-lateral and dorsal rays; dorsal lobe of bursa lacks bosses; female tail 0.22–0.28 mm; ovejector J-shaped.

***Coronostrongylus spearei* Beveridge, 2002**

Coronostrongylus spearei Beveridge, 2002a, 909–911, figs 53–61.

Type data: holotype SAM AHC 31498, allotype SAM AHC 31499, paratypes SAM AHC 25892–4, 25901, BMNH 2002.2.18.10–11, USNPC 91778.

Type locality: Doido, PNG (6°33′S 144°50′E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

Other hosts: *Dorcopsis hageni* Heller, 1897; *Dorcopsis muelleri* (Shlegel, 1866).

Site in host: stomach.

Distribution: PNG.

Diagnostic features: Males: 5.1–7.3 mm; females 5.6–7.9 mm; buccal capsule wider than long; 24 longitudinal pleats in buccal capsule; deirid in middle of oesophageal corpus; spicules 1.11–1.23 mm; externo-dorsal ray arises from lateral trunk; female tail 0.35–0.49 mm; ovejector J-shaped.

***Coronostrongylus spratti* Beveridge, 2002**

Coronostrongylus spratti Beveridge, 2002a, 911–913, figs 62–70.

C.oronostrongylus coronatus pro parte: Beveridge et al., 1989, p. 277.

Type data: holotype SAM AHC 31500, allotype SAM AHC 31501, paratypes SAM AHC 14415–6, BMNH 2002.2.18.12–13, USNPC 91779.

Type locality: Franklin Bay, Cape Upstart, Qld (19°42′S 147°45′E).

Type host: *Petrogale inornata* Gould, 1842.

Other hosts: *Petrogale assimilis* Ramsay, 1877.

Site in host: stomach.

Distribution: north-eastern Qld. Map: Beveridge, 2002a, p. 911.

Diagnostic features: Males: 3.2–5.1 mm; females 5.1–6.7 mm; buccal capsule longer than wide; c. 40 longitudinal pleats in buccal capsule; deirid immediately anterior to nerve ring; spicules 1.11–1.40 mm; externo-dorsal ray arises between postero-lateral and dorsal rays; dorsal lobe with sclerotized bosses; female tail 0.20–0.36 mm; ovejector J-shaped.

Cyclostrongylus Johnston & Mawson, 1939

Type species: *Cy. wallabiae* Johnston & Mawson, 1939.

Other species: *Cy. alatus* Beveridge, 1982; *Cy. elegans* Beveridge, 1982; *Cy. irma* Appan, Bergfeld & Beveridge, 2004; *Cy. kartana* (Mawson, 1955); *Cy. leptos* (Mawson, 1965); *Cy. parma* Johnston & Mawson, 1939; *Cy. perplexus* Beveridge, 1982.

Generic diagnosis: nematodes coiled dextrally or sinistrally, occasionally straight; with single ventral ala or two lateral alae; cephalic collar present; labial collar absent; cephalic papillae slightly domed with single, short seta; buccal capsule heavily sclerotized, circular in cross section, with prominent transverse striations; oesophagus short with prominent isthmus; bulb with 3 pairs of sclerotized plates in lining; nerve ring at level of oesophageal isthmus; deirid and excretory pore at level of oesophageal bulb; spicules elongate, alate; gubernaculum absent; bursa without sclerotised bosses; vulva immediately anterior to anus; ovejector J-shaped.

Comments: Although well defined morphologically by the buccal capsule, oesophagus, coiled habit and presence of alae as well as its site of occurrence in the oesphagus of the host rather than the stomach (Beveridge, 1982), more recent molecular studies (Chilton et al., 2016b, Beveridge et al., 2020) have not eliminated the possibility that the genus may be polyphyletic. Most species can be identified based on the features of the buccal capsule. However, in some closely related species (*Cy. kartana*, *Cy. elegans*) the morphology of the spicule tip is the most reliable distinguishing feature.

Key to species of Cyclostrongylus

1a. Buccal capsule long and narrow; ratio of length to maximum width 2.9–4.5 2

1b. Buccal casule relatively shorter; ratio of length to maximum width 0.6–1. 5

2a. Buccal capsule of uniform diameter throughout; transverse striations regular (Figs 18 B–D) . . . 3

2b. Buccal capsule wider at anterior extremity; transverse striations faint and irregular anteriorly (Fig. 18 E) . . . . . *Cy. perplexus*

3a. Straight nematodes with paired lateral alae (Fig. 18F) . . . . . *Cy. alatus*

3b. Coiled nematodes with single ventral ala (Fig. 18 G) 4

4a. Ala of spicule terminates abruptly (Fig. 18 M); external branchlets of dorsal ray prominent; female tail <0.12 mm . . . . . *Cy. kartana*

4b. Ala of spicule diminishes gradually towards tip (Fig. 18 O); external branchlets of dorsal ray vestigial; female tail > 0.18 mm . . . *Cy. elegans*

5a. Buccal capsule wider than long (Fig. 18 K) . . . . . *Cy. parma*
5b. Buccal capsule longer than wide 6

6a. Buccal capsule of relatively uniform diameter throughout (Fig. 18 L) . . . . . *Cy. leptos*
6b. Buccal capsule wider at anterior extremity (Figs 18 I, J) 7

7a. Spicules 1.25–1.48 mm . . . . . *Cy. irma*
7b. Spicules 0.94–1.10 mm . . . . . *Cy. wallabiae*

***Cyclostrongylus alatus* Beveridge, 1982**

Cyclostrongylus alatus Beveridge, 1982, pp. 93–94, figs 331–339; Aussavy et al., 2011; p.16; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p.241.
Type data: holotype SAM V1768, allotype SAM V1769, paratypes SAM V1770–1779, AHC 10393; BMNH 1980.865–874; USNPC 75135.
Type locality: Swanfels, Qld (28° 11'S 152° 16'E).
Type host: *Notamacropus rufogriseus* (Desmarest, 1817).
Site in host: oesophagus.
Distribution: Qld, NSW, Vic, Tas.
Representative DNA sequence data: ITS1, 2: LN846133–4.
Diagnostic features (Figs 18 B, F, N, 45 B): Males 4.7–7.0 mm; females 6.7–7.5 mm; straight worms; paired lateral alae present; buccal capsule elongate, of uniform diameter, with regular transverse striations; spicules 0.82–0.98 mm; spicule ala terminates abruptly at spicule tip; female tail prominently truncated; ovejector J-shaped.
Comments: this species is located in the anterior part of the oesophagus in a region with plate–like papillae arranged in longitudinal rows with the nematodes lying between the rows of papillae (Beveridge, 1982).

***Cyclostrongylus elegans* Beveridge, 1982**

Cyclostrongylus elegans Beveridge, 1982, pp. 97–98, figs 351–361; Beveridge et al., 1998, p. 482.
Type data: holotype SAM V1792, allotype SAM V1793, paratypes SAM V1794–1803, AHC 10392, BMNH 1979.861–864, USNPC 75134.
Type locality: Rivertree, NSW (28° 39'S 152° 18'E).
Type host: *Notamacropus parryi* (Bennett, 1835).
Site in host: oesophagus.
Distribution: eastern Qld, north-eastern NSW.
Representative DNA sequence data: ITS1, 2: LN846135.
Diagnostic features (Figs 18 A, C, O): Males 6.6–9.0 mm; females 8.1–9.3 mm; nematodes coiled sinistrally; single ventral ala present; buccal capsule elongate, of uniform diameter, with regular transverse striations; dorsal ray with vestigial external branchlets; spicules 0.97–1.16 mm; spicule ala diminishes gradually towards spicule tip; female tail conical, 0.18–0.22 mm; ovejector J-shaped.

***Cyclostrongylus irma* Appan, Bergfeld & Beveridge, 2004**

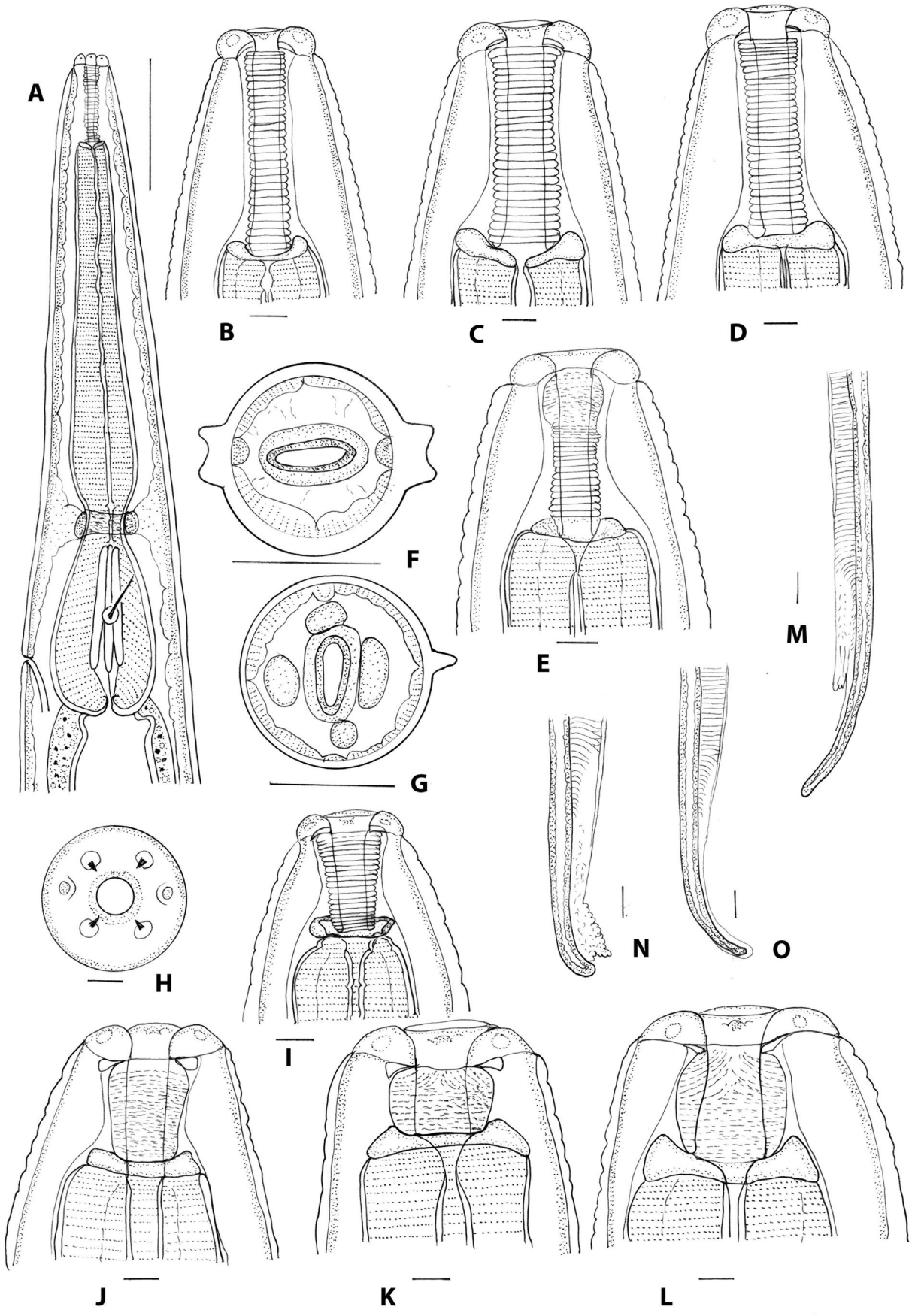
Cyclostrongylus irma Appan, Bergfeld & Beveridge, 2004, pp. 80–82, figs 15–24.
Type data: holotype SAM AHC 32185, allotype SAM AHC 32186, paratypes SAM AHC 32187, BMNH 2003.2.7.3–4, USNPC 93587.
Type locality: Collie, WA (33° 22'S 116° 09'E).
Type host: *Notamacropus irma* (Jourdan, 1837).
Site in host: oesophagus.
Distribution: south-western WA.
Representative DNA sequence data: ITS1, 2: LN846136–7.
Diagnostic features (Fig. 18 J): Males 8.8–9.8 mm; females 9.6–11.6 mm; nematodes coiled; single ventral ala present; buccal capsule short, length: width ratio 1.3, slightly wider anteriorly, with irregular, faint transverse striations; spicules 1.25–1.48 mm; spicule ala diminishes gradually towards spicule tip; female tail conical; ovejector J-shaped.

***Cyclostrongylus kartana* (Mawson, 1955)**

Spirostrongylus kartana Mawson, 1955, pp. 2–3, figs 3–6.
Oesophagonastes kartana: Mawson, 1965, p. 157; Smales & Mawson, 1978a, p. 11–13, 1978b, pp. 80–81.
Cyclostrongylus kartana: Mawson, 1977a, p. 20; Beveridge, 1982, pp. 94–96, figs 340–350; Spratt & Beveridge, 2016, p. 139.

Fig. 18. Genus *Cyclostrongylus*. A, *Cyclostrongylus alatus*, anterior end, lateral view; B, *Cy. alatus*, buccal capsule, lateral view; C, *Cy. elegans*, buccal capsule, lateral view; D, *Cy. kartana*, buccal capsule, lateral view; E, *Cy. perplexus*, buccal capsule, lateral view; F, *Cy. alatus*, transverse section of mid-body region showing paired lateral alae; G, *Cy. perplexus*, transverse section of mid-body region showing single ventral ala; H, *Cy. perplexus*, anterior end, apical view; I, *Cy. wallabiae*, buccal capsule, lateral view; J, *Cy. irma*, buccal capsule, lateral view; K, *Cy. parma*, buccal capsule, lateral view; L, *Cy. leptos*, buccal capsule, lateral view; M, *Cy. kartana*, spicule tip, lateral view; N, *Cy. alatus*, spicule tip, lateral view; O, *Cy. elegans*, spicule tip, lateral view. (A–I; K–O from Beveridge, 1982; J, from Appan et al., 2004).

Scale-bars: A, F, G, 0.1 mm, B–E, H–O, 0.01 mm.


A
B
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Type data: syntypes SAM AHC 70.
Type locality: Kangaroo Island, SA (35° 45′S 137° 00′E).
Type host: *Notamacropus eugenii* (Desmarest, 1817).
Other hosts: *Notamacropus irma* (Jourdan, 1837).
Site in host: oesophagus.
Distribution: SA (Kangaroo Island); south-western WA.
Representative DNA sequence data: ITS1, 2: LN846133–9.
Diagnostic features (Figs 18 D, M): Males 7.2–8.4 mm; females 9.0–9.5 mm; nematodes coiled dextrally; single ventral ala present; buccal capsule elongate, of uniform diameter, with regular transverse striations; spicules 0.76–0.95 mm; spicule ala terminates abruptly anterior to spicule tip; female tail conical, 0.06–0.12 mm; ovejector J-shaped.
Comments: This species is primarily parasitic in the oesophagus of *N. eugenii* in South and Western Australia, but has also been reported from *N. irma* in Western Australia where the two host species occur in sympatry. There are records in SAM of this species in captive *N. parma* (SAM 8185, 10898), but the wallabies may have been held in the same enclosures as *N. eugenii*.

***Cyclostrongylus leptos* (Mawson, 1965)**
Oesophagonastes leptos Mawson, 1965, pp. 159–161, figs 54–58.
Cyclostrongylus leptos: Mawson, 1977a, p. 20; Beveridge, 1982, pp. 98–100, figs 362–367; Beveridge et al., 1998, p. 482.
Type data: holotype SAM V1702, allotype SAM V1703, paratypes SAM AHC 6292.
Type locality: Logan Village, Qld (27° 46′S 153° 06′E).
Type host: *Notamacropus dorsalis* (Gray, 1837).
Site in host: oesophagus.
Distribution: Qld.
Representative DNA sequence data: ITS1, 2: LN846140.
Diagnostic features (Fig. 18 L): Male (holotype) 9.1 mm; females 10–8–12.6 mm; nematodes coiled; single ventral ala present; buccal capsule short, length: width ratio 1.3, not wider anteriorly, with irregular, faint transverse striations; oesophageal bulb slender; spicules 0.90 mm; female tail slender, conical 0.27–0.31 mm; ovejector J-shaped.
Comments: *Cyclostrongylus leptos* apparently occurs infrequently in its only host, *N. dorsalis* (see Beveridge et al., 1998). The current description (Beveridge, 1982) is incomplete and details of the spicule tips and mouth opening remain to be determined.

***Cyclostrongylus parma* (Johnston & Mawson, 1939)**
Pharyngostrongylus parma Johnston & Mawson, 1939b, p. 516, figs 5–7; Popova, 1958, pp. 248–249, fig. 168.
Spirostrongylus parma: Mawson, 1955, p. 2.
Rugopharynx parma: Yamaguti, 1961, p. 410.
Oesophagonastes parma: Mawson, 1965, p. 159, fig. 53.
Cyclostrongylus parma: Mawson, 1977a, p. 20: Beveridge, 1982, pp. 100–101, figs 368–371.
Type data: holotype and allotype (tail only), SAM AHC 42828.
Type locality: Narara, NSW (33° 24′S 151° 21′E).
Type host: *Notamacropus parma* (Waterhouse, 1846).
Site in host: oesophagus.
Distribution: NSW.
Diagnostic features (Fig. 18 K): Nematodes coiled; single ventral ala present; buccal capsule wider than long, length: width ratio 0.6, not wider anteriorly, with irregular, faint transverse striations; oesophageal bulb slender; spicules 0.92 mm.
Comments: This species is known only from a single male and the tail of one female, both in poor condition. It is recognisable based on the extremely short buccal capsule which is wider than long.

***Cyclostrongylus perplexus* Beveridge, 1982**
Cyclostrongylus perplexus Beveridge, 1982, pp. 89–90, figs 304–314; Aussavy et al., 2011; p.16; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 241.
Type data: holotype SAM V1780, allotype SAM V1781, paratypes SAM V1782–1791, AHC 41780–41791, BMNH 1979.851–860, USNPC 75133.
Type locality: Grampian Ranges, Vic (37° 25′S 142° 20′E).
Type host: *Notamacropus rufogriseus* (Desmarest, 1817).
Site in host: oesophagus.
Distribution: Qld, NSW, Vic, SA, Tas.
Representative DNA sequence data: ITS1, 2: LN846141–5.
Diagnostic features (Figs 18 E–H): Males 5.4–9.0 mm; females 8.0–10.7 mm; nematodes coiled; single ventral ala present; buccal capsule elongate, broader in diameter at anterior end; regular transverse striations in posterior part becoming finer and irregular in anterior region; spicules 0.70–1.00 mm; spicule ala diminishing gradually towards spicule tip; female tail conical, very short, 0.035–0.045 mm; ovejector J-shaped.
Comments: This species occurs in the more posterior regions of the oesophagus, coiled around elongate papillae (Beveridge, 1982).

***Cyclostrongylus wallabiae* Johnston & Mawson, 1939**

Cyclostrongylus wallabiae Johnston & Mawson, 1939b, pp. 517–518, figs 8–10; Yamaguti, 1961, p. 408; Mawson, 1977a, pp. 19–20; Popova, 1960, pp.76–77, fig. 46; Beveridge, 1982, pp. 91–93, figs 315–330; Beveridge et al., 1985, p. 378; 1998, p. 482; Aussavy et al., p.17; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 211; Spratt et al., 2017, p. 242.

Pharyngostrongylus gallardi Johnston & Mawson, 1942, pp. 110–111, figs 1–4; Popova, 1958, pp. 244–245, fig. 162.

Spirostrongylus gallardi: Mawson, 1955, p. 2.

Rugopharynx gallardi: Yamaguti, 1961, p. 410.

Oesophagonastes gallardi: Magzoub, 1964, pp. 48–49, figs 1–7; Mawson, 1965, pp. 157, 159.

Type data: holotype and allotype, SAM AHC 42818.

Type locality: Lower Hawkesbury, NSW (33° 30′S 151° 10′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: oesophagus.

Distribution: Qld, NSW, Vic.

Representative DNA sequence data: ITS1, 2: LN846146–8.

Diagnostic features (Fig. 18 I): Males 9.8–11.8 mm; females 10.6–13.7 mm; nematodes coiled; single ventral ala present; buccal capsule slightly longer than wide, length: width ratio 1.6; broader in diameter at anterior end; transverse striations regular; dorsal lobe of bursa elongate; spicules 0.94–1.10 mm; spicule ala diminishing gradually towards spicule tip; posterior end of female swollen; female tail conical; ovejector Jshaped.

Dorcopsinema Mawson, 1977

Type species: *D. dorcopsis* (Baylis, 1940).

Other species: *D. amplum* Purwaningsih & Smales, 2018; *D. dendrolagi* Smales, 1982; *D. longispiculare* Purwaningsih & Smales, 2014; *D. mbaiso* Smales, 1997; *D. simile* Smales, 1999.

Generic diagnosis: cephalic collar prominent or almost absent; cephalic papillae domed, with single short seta; amphids mounted on prominent elevations; 6 or 8 lips at mouth opening; buccal capsule short, sclerotized, circular in cross section; oesophageal corpus elongate, clavate; deirid, nerve ring and excretory pore in anterior oesophageal region; anterior extremity of intestine projects slightly anteriorly with dorsal and ventral lobes overlapping oesophagus; bursa without bosses on surface; external branchlets of dorsal ray arising at principal bifurcation, shorter than internal branchlets; spicules elongate, alate; gubernaculum present; ovejector J-shaped.

Comments: Members of this genus from tree kangaroos (*Dendrolagus* spp.) are readily distinguishable from those in forest wallabies (*Dorcopsis* spp., *Dorcopulus* spp.) in that the former have six lips while the latter have eight lips. The nematode species from Papua New Guinea in *Dc. dorcopsis* and *Dp. vanheurni* are very similar and differ primarily in measurements, while the nematodes from Western New Guinea in the host *Dc. muelleri* (*D. amplum*, *D. longispiculare*) differ primarily in the features of the spicules. A single male nematode specimen in SAM (46515) from *Dc. muelleri* from Salawati Island, Western New Guinea, has a distinctive dorsal ray (Fig. 20 D) suggesting that additional species may be present within this genus.

Key to species of Dorcopsinema

(Modified from Purwaningsih & Smales, 2014, 2018)

1a. Cephalic collar clearly demarcated from body by greater width and distinct suture (Fig. 19 B) . . 2

1b. Cephalic collar not clearly demarcated from body by greater width and distinct suture (Fig. 19 F) . . . . . *D. dendrolagi*

2a. External branchlets of dorsal ray vestigial (Fig. 20 A) . . . . . *D. mbaiso*

2b. External branchlets of dorsal ray prominent . . . 3

3a. Deirids posterior to nerve ring; external branchlets of dorsal ray arise anterior to major bifurcation (Figs 20 B, C) 4

3b. Deirids anterior to nerve ring; external branchlets of dorsal ray arise posterior to major bifurcation (Fig. 19 F) . . . . . *D. dorcopsis*

4a. Spicule ala diminishes towards spicule tip . . . . . *D. longispiculare*

4b. Spicule ala terminates anterior to tip 5

5a. Principal bifurcation of dorsal ray at one third of its length (Fig. 20 C) . . . . . *D. amplum*

5b. Principal bifurcation of dorsal ray at one half of its length . . . . . *D. simile*

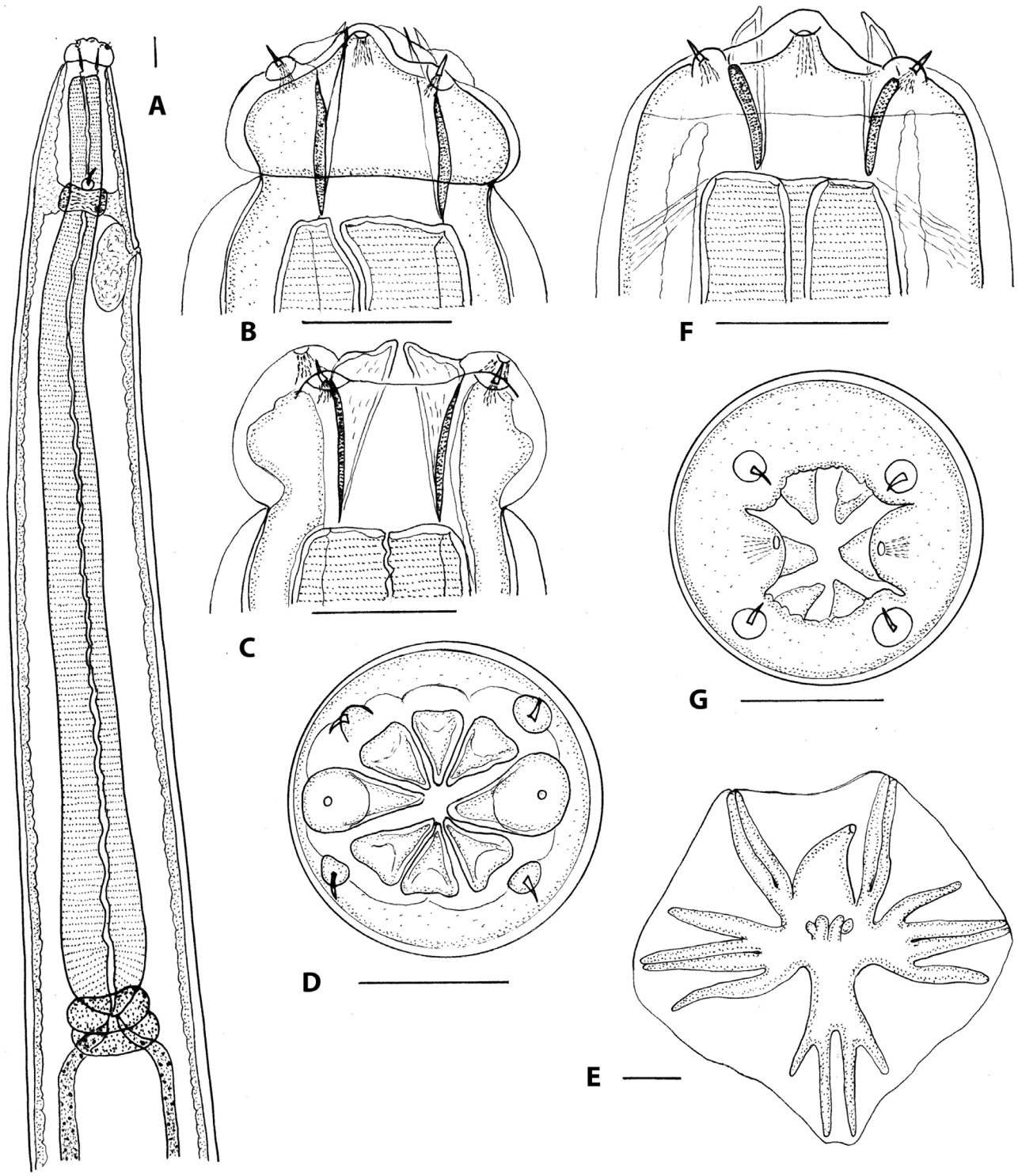


Fig. 19. Genus *Dorcopsinema*. A, *Dorcopsinema dorcopsis*, anterior end, lateral view; B, *D. dorcopsis*, buccal capsule, lateral view; C, *D. dorcopsis*, buccal capsule, dorsal view; D, *D. dorcopsis*, mouth opening, apical view; E, *D. dorcopsis*, bursa, apical view; F, *Dorcopsinema dendrolagi*, buccal capsule, lateral view; G, *D. dendrolagi,* mouth opening, apical view. (A–F, original; G from Smales, 1982a).

Scale-bars: 0.1 mm.

***Dorsopsinema amplum* Purwaningsih & Smales, 2018**

Dorsopsinema amplum Purwaningsih & Smales, 2018, pp. 63–66, figs 3 A–K, 4 E–F.

Type data: holotype, allotype MZB Na 743, paratypes MZB Na 744.

Type locality: Lengguru, Western New Guinea (1° 6′S 130° 51′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea .

Diagnostic features (Fig. 20 C): Males 19.6–24.9 mm; females 23.9–44.1 mm; distinct cephalic collar present; 8 lips; spicules 1.95–2.22 mm; ala diminishes in width to tip; ovejector J-shaped.

***Dorcopsinema dendrolagi* Smales, 1982**

Dorcopsinema dendrolagi Smales, 1982a, pp. 366, 368, figs 28–37; Flannery et al., 1996, p. 187; Smales 1997a, p. 132; 1999, p. 140; Smales 2006, p. 98; Purwaningsih & Smales, 2014, p. 597; 2018, p. 68.

Type data: holotype BMNH 1981.4565, allotype BMNH 1981.4566, paratypes BMNH 1981.4567–4616, SAM AHC 8987.

Type locality: Lake Trist, PNG (7° 29′S 146° 58′E).

Type host: *Dendrolagus goodfellowi* Thomas, 1908.

Other hosts: *Dendrolagus dorianus* Ramsay, 1883; *Dendrolagus inustus* Müller, 1840; *Dendrolagus scottae* Flannery & Seri, 1990.

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 19 F, G): Males 24.0–30.0 mm; females 35.0–42.0 mm; cephalic collar poorly defined; 6 lips; spicules 1.33–1.53 mm; ala terminates anterior to tip; ovejector J-shaped.

Comments: *Dendrolagus matschiei* and *Dend. mbaiso* were incorrectly cited as additional hosts by Spratt & Beveridge (2016).

***Dorcopsinema dorcopsis* (Baylis, 1940)**

Macropostrongylus dorcopsis Baylis, 1940, pp. 313–318, figs 1–5: Skrjabin et al., 1952, p. 291.

Gelanostrongylus dorcopsis: Popova, 1960, 84–86, figs 52, 53; Yamaguti, 1961, p. 405;

Dorcopsinema dorcopsis: Mawson, 1977b, p. 61, figs 45–46, 53; Smales, 1982a, pp. 367–368, figs 22–27; 1999, p. 140; 2006, p. 98; Purwaningsih & Smales, 2014, p. 596; 2018, p. 68.

Type data: syntypes BMNH 1942.10.21.271–285.

Type locality: Yapen (or Japen) Island, Western New Guinea (1° 45′S 136° 08′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866) (as *D. veterum* (Lesson, 1827)).

Other hosts: *Dorcopsis luctuosa* (D'Albertis, 1874) (as *D. veterum* (Lesson, 1827)).

Site in host: stomach.

Distribution: PNG; Western New Guinea.

Diagnostic features (Figs 19 A–E): Males 19.0–25.0 mm; females 30.0–35.0 mm; distinct cephalic collar present; 8 lips; spicules 1.87–2.38 mm; ala diminishes gradually to tip; ovejector J-shaped.

Comments: The nomenclature of the species of *Dorcopsis* acting as hosts of *D. dorcopsis* was clarified by Smales (1997a, p. 131). The current identifications are based on the locations at which specimens were collected and the currently known distributions of the host species (Flannery, 1995).

***Dorcopsinema longispiculare* Purwaningsih & Smales, 2014 (orth. emend.)**

Dorcopsinema longispicularis Purwaningsih & Smales, 2014, pp. 529–594, figs 1–13, 27–28; 2018, p. 68.

Type data: holotype, allotype MZB Na 641, paratypes MZB Na 642.

Type locality: Raja Ampat Island, Western New Guinea (1° 06′S 130° 51′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea .

Diagnostic features (Fig. 20 B): Males 8.3–10.3 mm; females 8.0–12.2 mm; distinct cephalic collar present; 8 lips; spicules 2.40–2.57 mm; ala terminates anterior to tip; ovejector J-shaped.

Comments: The spelling of the specific name has been emended as *Dorcopsinema* is a neuter noun.

***Dorcopsinema mbaiso* Smales, 1997**

Dorcopsinema mbaiso Smales, 1997a, pp. 132–134, figs 1–15; 1999, p. 140; 2006, p. 98; Purwaningsih & Smales, 2014, p. 596; 2018, p. 68.

Type data: holotype SAM AHC 30458, allotype SAM AHC 30459, paratypes SAM AHC 30460.

Type locality: Gunung Ki, Tembagapura, Western New Guinea (4° 05′S 137° 06′E).

Type host: *Dendrolagus mbaiso* Flannery, Boeadi & Szaley, 1995.

Site in host: stomach.

Distribution: Western New Guinea.

Diagnostic features (Fig. 20 A): Males 12.0–15.0 mm; females 19.0–22.0 mm; distinct cephalic collar present; 6 lips; deirid post–buccal; dorsal lobe of bursa elongate; external branchlets of dorsal ray vestigial; spicules 0.82–1.26 mm; ala diminishes to tip; ovejector J-shaped.

***Dorcopsinema simile* Smales, 1999**

Dorcopsinema simile Smales, 1999, pp. 138–140, figs 1–22; 2006, p. 98; Purwaningsih & Smales, 2014, p. 596; 2018, p. 68.

Type data: holotype SAM AHC 31326, allotype SAM AHC 31327, paratypes SAM AHC 31328.

Type locality: Doido, Chimbu Province, PNG (6° 33'S 144° 50'E).

Type host: *Dorcopsulus vanheurni* (Thomas, 1922).

Site in host: stomach.

Distribution: PNG.

Diagnostic features: Males 16.0–24.0 mm; females 28.0–32.0 mm; distinct cephalic collar present; 8 lips; spicules 1.69–2.06 mm; ala terminates anterior to tip; ovejector J-shaped.

Comments: This specied is very similar to *D. dorcopsis*, differing only in measurements. Smales (1999) also reported specimens from *Dorcopsulus* sp. from Lae, PNG. Based on know distributions, this host will also be *D. vanheurni*.

Dorcopsistrongylus Smales, 1982

Type species: *Do. labiacarinatus* Smales, 1982.

Other species: *Do. ewini* Purwaningsih & Smales, 2010; *Do. salawatiensis* Purwaningsih & Smales, 2010; *Do. supriyatnai* Purwaningsih, Dewi & Smales, 2019.

Generic diagnosis: cephalic collar present; cephalic papillae domed, with short setae; labial crown consisting of 4 elements, petaloid; amphids mounted on base of labial crown elements, cephalic papillae between labial crown elements; buccal capsule heavily sclerotized, circular in cross section, with numerous transverse striations; oesophageal corpus elongate; oesophageal bulb elongate, clavate; deirid in anterior oesophageal region; anterior extremity of intestine projects anteriorly with dorsal and ventral lobes enveloping oesophageal bulb (except in *Do. supriyatnai*); bursa without bosses on surface; spicules elongate, alate; gubernaculum present; ovejector Y- or J-shaped.

Key to species of Dorcopsistrongylus

1a. Intestinal lobes absent . . . . . *Do. supriyatnai*
1b. Intestinal lobes present (Fig. 20 E) 2

2a. Anterior end of spicule with prominent twist . . . . . *Do. ewini*
2b. Anterior end of spicule without prominent twist 3

3a. Labial collar with fine longitudinal striations . . . . . *Do. labiacarinatus*
3b. Labial collar without fine longitudinal striations . . . . . *Do. salawatiensis*

***Dorcopsistrongylus ewini* Purwaningsih & Smales, 2010**

Dorcopsistrongylus ewini Purwaningsih & Smales, 2010, pp. 596–598, figs 1–14, 30.

Type data: holotype, allotype MZB Na 415, paratypes MZB Na 416.

Type locality: Salawati Island, Western New Guinea (1° 6'S 130° 51'E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

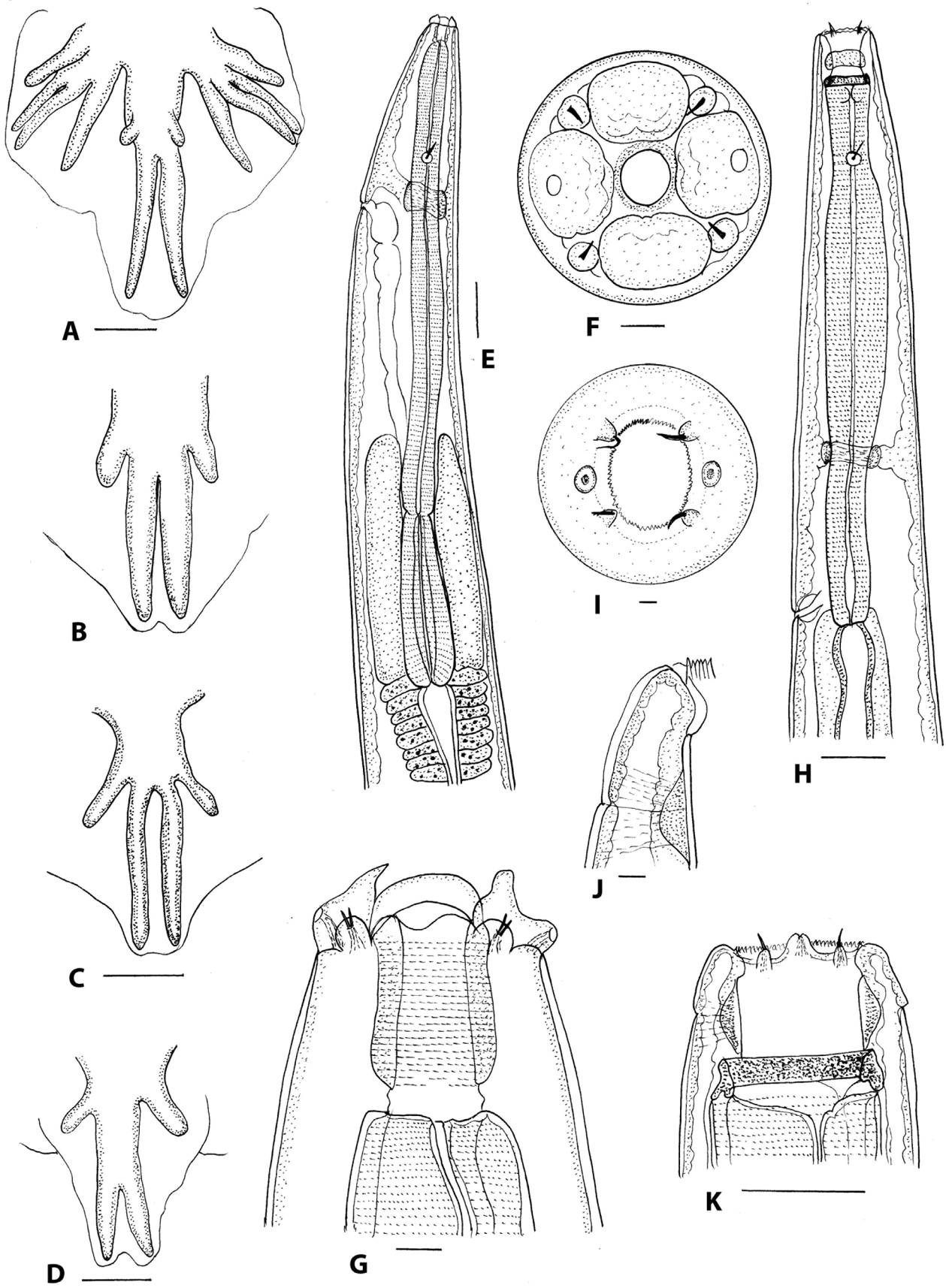
Site in host: stomach.

Distribution: Western New Guinea.

Diagnostic features: Males 4.4–6.5 mm; females 6.4–9.1 mm; labial collar without fine longitudinal striations; lateral elements of labial crown not subdivided medially; intestinal lobes present; anterior end of spicule with prominent twist; vagina long, sinuous, thick-walled, ovejector J-shaped.

Fig. 20. Genera *Dorcopsinema*, *Dorcopsistrongylus*, *Foliostoma*. A, *Dorcopsinema mbaiso*, bursa, dorsal view; B, *Dorcopsinema longispiculare*, dorsal ray of bursa, dorsal view; C, *Dorcopsinema amplum*, dorsal ray of bursa, dorsal view; D, *Dorcopsinema* sp. (SAM AHC 46515), dorsal ray of bursa, dorsal view; E, *Dorcopsistrongylus labiacarinatus*, anterior end, lateral view; F, *Do. labiacarinatus*, mouth opening, apical view; G, *Do. labiacarinatus*, buccal capsule, dorsal view; H, *Foliostoma macropodis*, anterior end, lateral view; I, *Foliostoma macropodis*, mouth opening, apical view; J, *F. macropodis*, optical section through mouth opening, lateral view, showing leaf crown; K, *F. macropodis*, buccal capsule, lateral view. (A, from Smales, 1997a; B, from Purwaningsih & Smales, 2014; C, from Purwaningsih & Smales, 2018; D–G, original; H–K from Beveridge & Johnston, 1981).

Scale-bars: A, D, 0.05 mm; C, 0.025 mm; E, H, I, K, 0.1 mm; F, G, J, 0.01 mm (no scale bar on original figure of 20B).


A
B
C
D
E
F
G
H
I
J
K

***Dorcopsistrongylus labiacarinatus* Smales, 1982**

Dorcopsistrongylus labiacarinatus Smales, 1982b, pp. 31–33, figs 1–10; 1999, p. 137; Spratt & Beveridge, 2016, p. 126.

Type data: holotype BMNH 1981.4537, allotype BMNH 1981.4538.

Type locality: Middle Strickland, PNG (7° 1′S 142° 12′E).

Type host: *Dorcopsis luctuosa* (D'Albertis, 1874) (as *D. veterum* Lesson, 1827).

Other hosts: *Dorcopsis hageni* Heller, 1897; *Dorcopsulus vanheurni* (Thomas, 1922).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 20 E–G): Males 6.0–10.0 mm; females 11.0 mm; labial collar with fine longitudinal striations; lateral elements of labial crown not subdivided medially; intestinal lobes present; anterior end of spicule without prominent twist; vagina short, thick-walled; ovejector Y-shaped.

***Dorcopsistrongylus salawatiensis* Purwaningsih & Smales, 2010**

Dorcopsistrongylus salawatiensis Purwaningsih & Smales, 2010, pp. 598–599, figs 15–29, 31.

Type data: holotype, allotype MZB Na 417, paratypes MZB Na 459.

Type locality: Salawati Island, Western New Guinea (1° 6′S 130° 51′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea .

Diagnostic features: Males 6.6–8.7 mm; females 8.0–10.6 mm; labial collar without fine longitudinal striations; lateral elements of labial crown subdivided medially; intestinal lobes present; anterior end of spicule without prominent twist; vagina sinuous, thick-walled; ovejector J-shaped.

***Dorcopsistrongylus supriyatnai* Purwaningsih, Dewi & Smales, 2019**

Dorcopsistrongylus supriyatnai Purwaningsih, Dewi & Smales, 2019, pp. 437–440, figs 16–28.

Type data: holotype, allotype MZB Na 764, paratypes MZB Na 765.

Type locality: Kumawa Mountains, Western New Guinea (1° 6′S 130° 51′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea.

Diagnostic features: Males 8.7–12.3 mm; females 8.3–19.0 mm; labial collar without fine longitudinal striations; lateral elements of labial crown not subdivided medially; intestinal lobes absent; anterior end of spicule without prominent twist; vagina long, sinuous; ovejector J-shaped.

Foliostoma Beveridge & Johnson, 1981

Type species: *F. macropodis* Beveridge & Johnson, 1981.

Generic diagnosis: cephalic collar absent; submedian papillae conical, with single seta; external leaf crown of tiny elements; buccal capsule slightly wider than long, dorso-ventrally elongate in apical view; internal surfaces of capsule parallel, external surfaces forming a single lobe at mid-length, without transverse striations; wall poorly sclerotized, supported externally by prominent radial muscles; prominent sclerotized annulus present at base of buccal capsule; oesophageal corpus narrower at anterior extremity, becoming wider; isthmus indistinct; bulb cylindrical; nerve ring at oesophageal isthmus; deirid immediately postbuccal; excretory pore at oesophago-intestinal junction; bursa with sclerotized bosses; spicules elongate, alate; gubernaculum present; vulva anterior to anus; ovejector J-shaped.

***Foliostoma macropodis* Beveridge & Johnson, 1981**

Foliostoma macropodis Beveridge & Johnson, 1981, pp. 84–84, figs 24–36, 38; Beveridge et al., 1992, p. 365; Griffith et al., 2000, p. 310.

Type data: holotype SAM V2027, allotype SAM V2028, paratypes SAM V2029–2033.

Type locality: Tolga, Qld. (17° 13′S 145° 29′E)

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, 2: MG 865625.

Diagnostic features (Figs 20 H–K): Males 6.5–9.0 mm; females 7.9–11.0 mm; spicules 2.17–2.48 mm; spicule ala terminates abruptly anterior to spicule tip; female tail 0.40–0.53 mm; ovejector J-shaped.

Labiomultiplex Smales, 1994

Type species: *Lm. eugenii* (Johnston & Mawson, 1940).

Other species: *Lm. billardierii* Smales, 1994; *Lm. constrictus* Smales, 1994; *Lm. contiguus* Chilton & Smales, 1996; *Lm. kimberleyensis* Smales, 1994; *Lm. novaeguineae* Smales, 1982; *Lm. onychogale* (Johnston

& Mawson, 1939); *Lm. potoroi* Smales, 1994; *Lm. sagawinensis* Purwaningsih & Smales, 2011; *Lm. thylogale* Smales, 1994; *Lm. uncinatus* (Johnston & Mawson, 1939).

Generic definition: cephalic collar absent; cervical cuticle not inflated; 6 large lips with pulp cavity present; sub-medial papillae and amphids borne on lips; interlabia absent; buccal capsule shallow, wider than long, without transverse striations; oesophagus claviform, corpus narrow anteriorly, widening posteriorly, isthmus indistinct, bulb very small, not lined with sclerotized plates; nerve ring encircles oesophageal isthmus; deirid in mid-oesophageal region; excretory pore at level of nerve ring; oesophago-intestinal diverticula present or absent; gubernaculum present; ovejector J-shaped.

Key to species of Labiomultiplex

1a. Oesophago-intestinal diverticula absent (Fig. 22 D) . . . . . .*Lm. kimberleyensis*
1b. Oesophago-intestinal diverticula present (Figs 21 A, 22 E–G) 2

2a. Spicules < 2.0 mm; oesophago-intestinal diverticula very small (Fig. 22 E) . . *Lm. thylogale*
2b. Spicules > 2.0 mm; oesophago-intestinal diverticula prominent 3

3a. Submedian lips with paired accessory lobes at base (Figs 21 C, 22 A) 4
3b. Submedian lips without paired accessory lobes at base 5

4a. Spicules < 3.0 mm . . . . . .*Lm. eugenii*
4b. Spicules > 3.0 mm . . . . . .*Lm. potoroi*

5a. Internal branches of dorsal ray as long as or only slightly longer than external branches (Figs 21 E, G) 6
5b. Internal branches of dorsal ray much longer than external branches (Figs 21 F, H) 9

6a. Spicules < 3.0 mm 7
6b. Spicules > 3.0 mm 8

7a. Spicules < 2.0 mm . . . . . *Lm. constrictus*
7b. Spicules > 2.0 mm . . . . . *Lm. thylogale*

8a. Buccal capsule shallow, length: width ratio 1.7 (Fig. 22 C) . . . . *Lm. onychogale*
8b. Buccal capsule deeper, length: width ratio 1.4 . . . . . *Lm. novaeguineae*

9a. Spicules > 4.0 mm . . . . . *Lm. billardierii*
9b. Spicules < 4.0 mm 10

10a. External branches of dorsal ray arise at level of principal bifurcation (Fig. 21 F) . *Lm. sagawinensis*
10b. External branches of dorsal ray arise posterior to principal bifurcation(Fig. 21 H . . 11

11a. Spicules > 3.2 mm; parasitic in *Notamacropus parryi* . . . . . *Lm. contiguus* *
10b. Spicules < 3.2 mm; parasitic in *Notamacropus dorsalis* . . . . . *Lm. uncinatus* *
* sibling species, can be difficult to differentiate morphologically

***Labiomultiplex billardierii* Smales, 1994**

Labiostrongylus (*Labiomultiplex*) *billardierii* Smales, 1994, pp. 202–204, figs 90–104.
Labiomultiplex billardierii: Smales, 2006, pp. 99–100.
Type data: holotype SAM V4518, allotype SAM V4519, paratypes SAM AHC 22809.
Type locality: Launceston, Tas. (41° 27′S 147° 10′E).
Type host: *Thylogale billardierii* (Desmarest, 1822).
Other hosts: *Notamacropus rufogriseus* (Desmarest, 1817).
Site in host: stomach.
Distribution: Tas; single record from Victoria before *Thyl. billardierii* became extinct in that state.
Representative DNA sequence data: ITS1, 2: FR854215.
Diagnostic features: Males 15–20 mm; females 19–25 mm; oesophago-intestinal diverticula present; submedian lips without paired accessory lobes at base, not bilobed at tips; dorsal lobe of bursa longer than lateral lobes; external branchlets arise posterior to principal bifurcation, directed anteriorly; spicules 4.00–4.70 mm; ala terminates anterior to tip; vagina sinuous; ovejector J-shaped.
Comments: The majority of records of this species are from *Thyl. billardierii*. The single record from *N. rufogriseus* is from an animal in an area of sympatry in Tasmania. The species has not been found in *N. rufogriseus* on the mainland (Aussavy et al., 2011; Vendl & Beveridge, 2014; Spratt et al., 2017).

***Labiomultiplex constrictus* Smales, 1994**

Labiostrongylus (*Labiomultiplex*) *constrictus* Smales, 1994, pp. 204–207, figs 105–117.

Labiomultiplex constrictus: Smales, 2006, p. 98.

Type data: holotype SAM V4162, allotype SAM V4163, paratypes SAM AHC 7331.

Type locality: Inkerman Station via Home Hill, Qld (19º 44'S 147º 28'E).

Type host: *Lagorchestes conspicillatus* Gould, 1842.

Site in host: stomach.

Distribution: north-eastern Qld.

Diagnostic features (Fig. 21 E): Males 17–24 mm; females 30–37 mm; oesophago-intestinal diverticula present; submedian lips without paired accessory lobes at base, not bilobed at tips; dorsal lobe of bursa no longer than lateral lobes; stem of dorsal ray elongate; external branchlets arise posterior to principal bifurcation, directed laterally; spicules 2.45–2.75 mm; ala terminates anterior to tip; vagina straight; ovejector J-shaped.

***Labiomultiplex contiguus* Chilton & Smales, 1996**

Labiostrongylus (*Labiomultiplex*) *contiguus* Chilton & Smales, 1996, pp. 51–53, figs 1, 3, 5–17; Beveridge et al., 1998, p. 482.

Labiomultiplex contiguus: Smales, 2006, p. 99.

Type data: holotype SAM AHC 30032, allotype SAM AHC 30089, paratypes SAM AHC 19999, 22802, 22806, 22814.

Type locality: Thangool, Qld (24° 29'S 150° 35'E).

Type host: *Notamacropus parryi* (Bennett, 1835).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, 2: FR854216.

Diagnostic features (Figs 21 D, 22 B, G): Males 20–24 mm; females 26–33 mm; oesophago-intestinal diverticula present; submedian lips without paired accessory lobes at base, not bilobed at tips; dorsal lobe of bursa no longer than lateral lobes; external branchlets of dorsal ray arise posterior to principal bifurcation, directed laterally; spicules 3.25–3.80 mm; ala diminishes gradually to tip; vagina straight; ovejector J-shaped.

***Labiomultiplex eugenii* (Johnston & Mawson, 1940)**

Zoniolaimus eugenii Johnston & Mawson, 1940b, p. 97; 1940c, pp. 360, 364, figs 8–12; Skrjabin et al., 1952, p. 174; Yamaguti, 1961, p. 403.

Labiostrongylus eugenii: Kung, 1948, pp. 104, 106; Popova, 1960, p. 97, fig. 63; Arundel et al., 1977, p. 142; Smales, 1977a, pp. 457–461; 1977b, pp. 449–456; Smales & Sommerville, 1977, pp. 205–209; Smales & Mawson, 1978a, p. 10; 1978b, p. 81; Richardson et al., 1987, p. 86 (as *Labiostrongylus* sp.).

Labiostrongylus (*Labiomultiplex*) *eugenii*: Smales, 1994, pp. 194–195, figs 47–58, 160, 161.

Labiomultiplex eugenii: Smales, 2002, p. 195; 2006, p. 98.

Type data: "cotypes" SAM AHC 3076, AM 1069.

Type locality: Deep Creek, Kangaroo Island, SA (35° 48' S 137° 13'E).

Type host: *Notamacropus eugenii* (Desmarest, 1817).

Site in host: stomach.

Distribution: SA (Kangaroo Island), south-western WA.

Representative DNA sequence data: ITS1, 2: FR854217–8.

Diagnostic features (Figs 21 A–C): Males 17–20 mm; females 25–30 mm; oesophago-intestinal diverticula present; submedian lips with paired accessory lobes at base, mildly bilobed at tips; dorsal lobe of bursa longer than lateral lobes; external branchlets arise posterior to major bifurcation, directed antero-laterally; spicules 2.58–2.90 mm; ala terminates anterior to tip; vagina sinuous; ovejector J-shaped.

***Labiomultiplex kimberleyensis* Smales, 1994**

Labiostrongylus (*Labiomultiplex*) *kimberleyensis* Smales, 1994, pp. 207–209, figs 118–130.

Labiomultiplex kimberleyensis: Smales, 2006, pp. 87–89, 99, figs 6–18.

Type data: holotype SAM V4164, allotype SAM V4165, paratypes SAM AHC 22810.

Type locality: Crystal Creek, Kimberley Division, WA (17° 09'S 124° 47'E).

Type host: *Onychogalea unguifera* (Gould, 1840).

Site in host: stomach.

Distribution: northern Qld, WA (Kimberley Division).

Diagnostic features (Fig. 22 D): Males 12–24 mm; females 14–38 mm; oesophago-intestinal diverticula absent; submedian lips without paired accessory lobes at base, not bilobed at tips; dorsal lobe of bursa longer than lateral lobes; external branchlets arise posterior to principal bifurcation, directed posteriorly; spicules 4.56–6.21 mm; ala terminates at tip; vagina elongate, straight; ovejector J-shaped.

***Labiomultiplex novaeguineae* Smales, 1982**

Labiostrongylus novaeguineae Smales, 1982a, pp. 364–365, figs 1–10, plate A, 1.

Labiostrongylus (*Labiomultiplex*) *novaeguineae*: Smales, 1984, pp 195–196.

Labiomultiplex novaeguineae: Smales, 2006, p. 98.

Type data: holotype BMNH 1981.4551, allotype BMNH 1981.4552, paratypes BMNH 1981.4553–62, SAM AHC 8986.

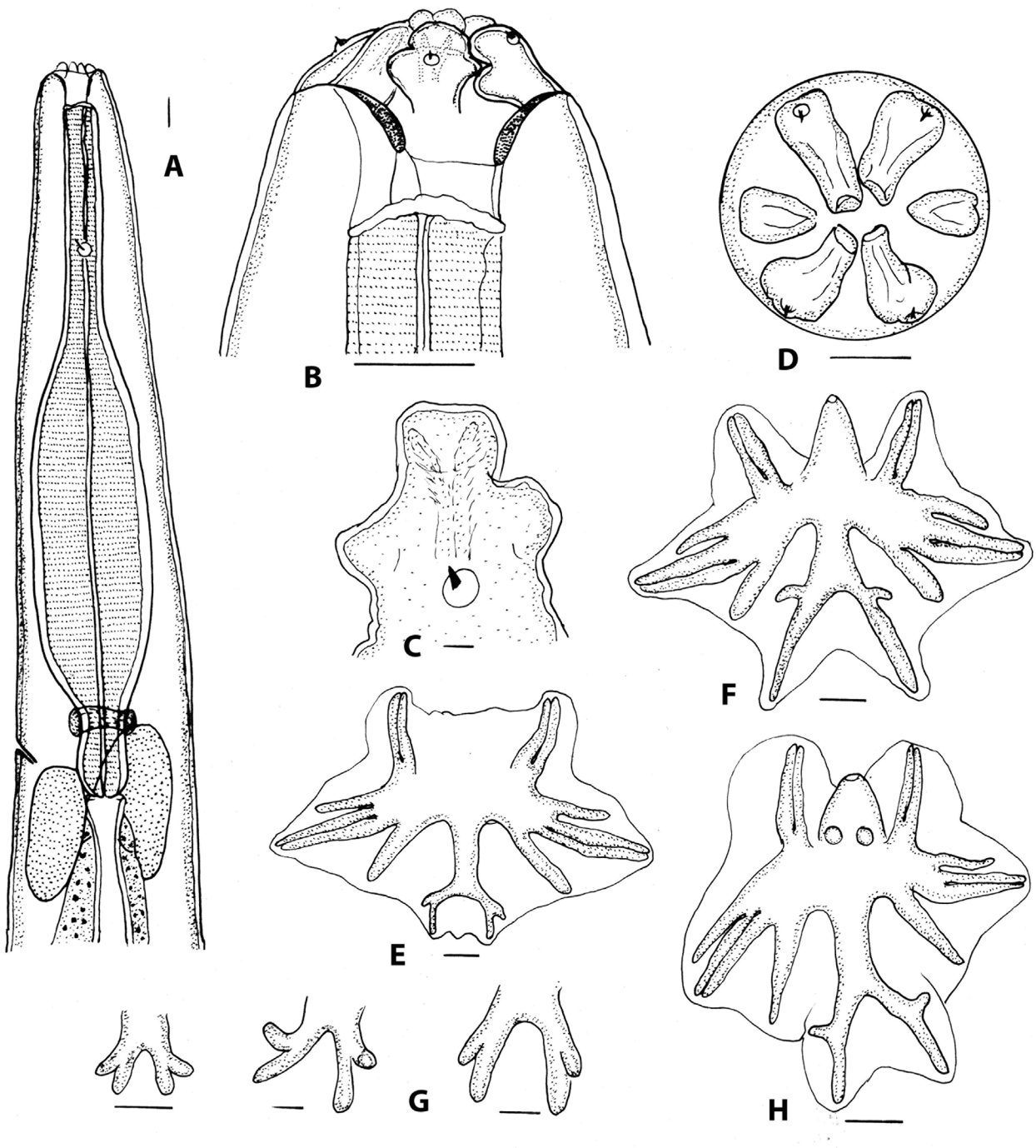


Fig. 21. Genus *Labiomultiplex*. A, *Labiomultiplex eugenii,* anterior end lateral view; B. *Lm. eugenii,* buccal capsule, oblique view; C, *Lm. eugenii,* sub-median lip with basal, lateral projections; D, *Labiomultiplex contiguus*, mouth opening, apical view; E, *Labiomultiplex constrictus*, bursa, apical view; F, *Labiomultiplex sagawinensis*, bursa, apical view; G, *Labiomultiplex onychogale*, three dorsal rays, dorsal view, showing variation in branching; H, *Labiomultiplex uncinatus*, bursa, apical view. (A–C, original; D, from Chilton & Smales, 1996; E, G–H, from Smales, 1994; F from Purwaningsih & Smales, 2011).

Scale-bars: A–D, 0.1mm; E, 0.08 mm; F, G, 0.05mm; H, 0.2 mm.

Type locality: Watabung, PNG (6° 05'S 145° 13'E).
Type host: *Dendrolagus* sp.
Site in host: stomach.
Distribution: PNG.
Diagnostic features: Males 12–15 mm; females 17–20 mm; oesophago-intestinal diverticula present; submedian lips without paired accessory lobes at base, bilobed at tips; dorsal lobe of bursa no longer than lateral lobes; external branchlets arise posterior to principal bifurcation; spicules 3.2–4.0 mm; ala terminates anterior to tip; vagina sinuous; ovejector J-shaped.

***Labiomultiplex onychogale* (Johnston & Mawson, 1939)**

Zoniolaimus onychogale Johnston & Mawson, 1939a, pp. 122, pp. 128–129, figs 13–15.
Labiostrongylus onychogale: Kung, 1948, pp. 104–106; Popova, 1960, p. 103; Beveridge et al., 1992, p. 365; Turni & Smales, 2001, p. 406.
Labiomultiplex (*Labiomultiplex*) *onychogale*: Smales, 1994, pp. 196–199, figs 59–75.
Labiomultiplex onychogale: Smales, 2006, p. 99.
Type data: holotype, allotype, 2 paratypes SAM AHC 41546.
Type locality: Upper Burnett River, Qld (24° 54'S 152° 23'E).
Type host: *Onychogalea fraenata* (Gould, 1840).
Other hosts: *Onychogalea unguifera* (Gould, 1840).
Site in host: stomach.
Distribution: eastern Queensland.
Representative DNA sequence data: ITS1, 2: FR854219.
Diagnostic features (Figs 21 G, 22 C): Males 11–15 mm; females 15–25 mm; oesophago-intestinal diverticula present; submedian lips without paired accessory lobes at base, not bilobed at tips; dorsal lobe of bursa no longer than lateral lobes; external branchlets arise posterior to principal bifurcation, all branchlets very short; spicules 3.9–5.3 mm; vagina straight; ovejector J-shaped.

***Labiomultiplex potoroi* Smales, 1994**

Labiostrongylus (*Labiomultiplex*) *potoroi* Smales, 1994, pp. 211–212, 214, figs 146–158.
Labiomultiplex potoroi: Smales, 2006, p. 100.
Type data: holotype SAM V4168, allotype SAM V4169, paratypes SAM AHC 4171.
Type locality: King Island, Tas (39° 52'S 143° 35'E).
Type host: *Potorous tridactylus* (Kerr, 1792).
Distribution: Tas.
Diagnostic features (Fig. 22 A): Males 16–20 mm; females 19–25 mm; oesophago-intestinal diverticula present; submedian lips with paired accessory lobes at base, mildly bilobed at tips; dorsal lobe of bursa no longer than lateral lobes; external branchlets of dorsal ray tiny, arise posterior to principal bifurcation; spicules 3.75–4.28 mm; ala terminates abruptly anterior to tip; vagina straight; ovejector J-shaped.

***Labiomultiplex sagawinensis* Purwaningsih & Smales, 2011**

Labiomultiplex sagawinensis Purwaningsih & Smales, 2011, pp. 127–130, figs 14–26, 31–32.
Type data: holotype, allotype MZB Na 491, paratypes MZB Na 492.
Type locality: Salawati Island, Western New Guinea (1° 06'S 130° 51'E).
Type host: *Dorcopsis muelleri* (Schlegel, 1866).
Site in host: stomach.
Distribution: Western New Guinea .
Diagnostic features (Fig. 21 F): Males 5.9–8.3 mm; females 16.2–17.8 mm; oesophago-intestinal diverticula present; submedian lips without paired accessory lobes at base, mildly bilobed at tips; dorsal lobe of bursa no longer than lateral lobes; external branchlets of dorsal arise posterior to principal bifurcation, directed laterally; internal branchlets long; spicules 2.08–3.36 mm; ala terminates anterior to tip; vagina straight; ovejector J-shaped.

***Labiomultiplex thylogale* Smales, 1994**

Labiostrongylus (*Labiomultiplex*) *thylogale* Smales, 1994, pp. 209–211, figs 131–145; Griffith et al., 2000, p. 310.
Labiomultiplex thylogale Smales, 2006, p. 100.
Type data: holotype SAM V4166, allotype SAM V4167, paratypes SAM AHC 10581.
Type host: *Thylogale stigmatica* (Gould), 1860.
Other hosts: *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: eastern Qld.
Representative DNA sequence data: ITS1, 2: FR854220.
Diagnostic features (Fig. 22 E): Males 16–24 mm; females 25–32 mm; oesophago-intestinal diverticula present, very small; submedian lips with 2 pairs of accessory lobes, at base and more distally, not bilobed at tips; dorsal lobe of bursa no longer than lateral lobes; external branchlets of dorsal arise posterior to principal bifurcation, directed posteriorly; spicules 1.75–1.98 mm; ala terminates abruptly anterior to tip; vagina straight; ovejector J-shaped.

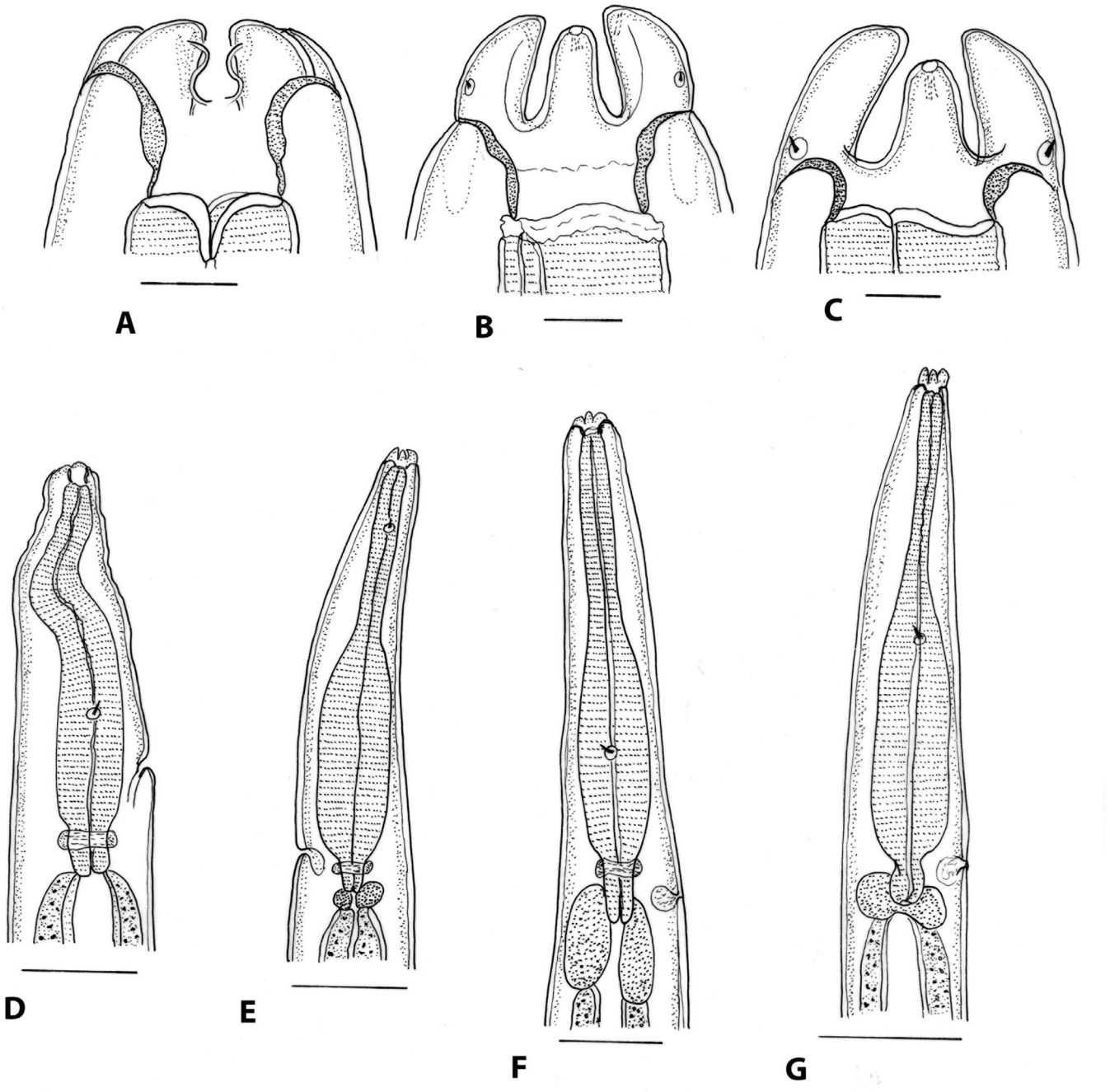


Fig. 22. Genus *Labiomultiplex*. A, *Labiomultiplex potoroi*, buccal capsule, dorso–ventral view; B, *Labiomultiplex contiguus*, buccal capsule, lateral view; C, *Labiomultiplex onychogale*, buccal capsule, lateral view; D, *Labiomultiplex kimberleyensis*, anterior end, lateral view; E, *Labiomultiplex thylogale*, anterior end, lateral view; F, *Lm. potoroi*, anterior end, lateral view; G, *Labiomultiplex contiguus*, anterior end, lateral view. (A, C–F, from Smales, 1994; B, G, from Chilton & Smales, 1996).

Scale-bars: A, 0.04 mm; B, 0.1mm; C, D, 0.05 mm; E, F, 0.08 mm; G, 1.0 mm.

***Labiomultiplex uncinatus* (Johnston & Mawson, 1939)**

Zoniolaimus uncinatus Johnston & Mawson, 1939a, pp. 127–129, figs 10–12; Skrjabin et al., 1952, p. 174; Popova, 1960, p. 105; Yamaguti, 1961, p. 404.

Labiostrongylus uncinatus: Kung, 1948, pp. 104, 106; Beveridge et al., 1998, p. 482.

Labiostrongylus (*Labiomultiplex*) *uncinatus*: Smales, 1994, pp. 199–202, figs 76–89; Smales & Chilton, 1996, p. 51, figs 2, 4.

Labiomultiplex uncinatus: Smales, 2006, p. 98.

Type data: holotype, allotype, paratypes, SAM V1545.

Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, 2: FR854221.

Diagnostic features (Fig 21 H): Males 18–25 mm; females 27–32 mm; oesophago-intestinal diverticula present; submedian lips without accessory lobes, not bilobed at tips; setae of submedial lips prominent, uncinate; dorsal lobe of bursa longer than lateral lobes; external branchlets of dorsal arise posterior to bifurcation, directed anteriorly; spicules 2.6–3.1 mm; ala terminates abruptly anterior to tip; vagina straight; ovejector J-shaped.

Comments: A record of this species from *Wal. bicolor* by Johnston & Mawson (1939a) cannot be confirmed as there are no specimens available (Smales, 1994). The species has not been encountered since in *Wal. bicolor* (see Beveridge, 2016). A single immature female of *Labiomultiplex* with characters similar to *Lm. uncinatus.* collected from *N. parma* from NSW is held in ANWC (N 1287) (Smales, 1995, p. 237; 2006, p. 99; Spratt & Beveridge, 2016, p. 139).

Labiosimplex Smales, 1994

Type species: *Ls. australis* (Kung, 1948).

Other species: *Ls. aridus* Smales, 1995; *Ls. bancrofti* (Johnston & Mawson, 1939); *Ls. bipapillosus* (Johnston & Mawson, 1939); *Ls. camporum* Smales, 2011; *Ls. centralis* Smales, 2006; *Ls. clelandi* (Johnston & Mawson, 1939); *Ls. communis* (Johnston & Mawson, 1939); *Ls. dendrolagi* Smales, 1995; *Ls. flanneryi* Smales, 1995; *Ls. godmani* Smales, 1995; *Ls. irma* Smales, 1995; *Ls. kungi* (Mawson, 1955); *Ls. laterilabellosus* Smales, 1995; *Ls. longispicularis* (Wood, 1929); *Ls. major* Smales, 1995; *Ls. mawsonae* Smales, 2011; *Ls. occidentalis* Smales, 1995; *Ls. papuensis* Purwaningsih & Smales, 2011; *Ls. pearsonensis* Smales, 1995; *Ls. petrogale* (Johnston & Mawson, 1938); *Ls. redmondi* (Smales, 1982); *Ls. robustus* Smales, 1995; *Ls. territoriensis* Smales, 2006; *Ls. thetidis* Smales, 1995; *Ls. thomasae* Smales, 1995; *Ls. turnbulli* Smales & Chilton, 1997.

Generic definition: cephalic collar absent; cervical cuticle not inflated; 6 large lips with pulp cavity; sub-median papillae and amphids borne on lips; interlabia absent; buccal capsule shallow, wider than long, without transverse striations; oesophagus claviform without distinct corpus, isthmus and bulb; nerve ring, deirid and excretory pore in anterior oesophageal region; oesophago-intestinal diverticula present; gubernaculum present; ovejector J- or Y-shaped.

Key to species of Labiosimplex

Due to overlapping spicule lengths, *Ls. pearsonensis* is included in two parts of the key.

1a. Lips triangular, pointed at tips (Figs 25H, I) . . . 2
1b. Lips blunt at tips, broad, quadrangular 3

2a. Spicules > 5 mm . . . . . *Ls. redmondi*
2b. Spicules < 5 mm . . . . . *Ls. papuensis*

3a. Spicules > 10 mm 4
3b. Spicules < 10 mm 7

4a. External branchlets of dorsal ray much longer than internals, extending almost to tips of internals (Fig. 25 A) . . . . . *Ls. pearsonensis*
4b. External branchlets of dorsal ray as long as internals, directed laterally 5

5a. Spicule tips curved, asymmetrical, right spicule thicker than left (Fig 24 F) . . . *Ls. longispicularis*
5b. Spicule tips straight, symmetrical 6

6a. External branchlets of dorsal ray arise anterior to major bifurcation (Fig. 24 H); oesophago-intestinal diverticula small (Fig. 24 G) . . *Ls. laterilabellosus*
6b. External branchlets of dorsal ray arise at or immediately anterior to major bifurcation (Fig. 24 I); oesophago-intestinal diverticula large (Fig. 24 K) . . . . . *Ls. major*

7a. External branchlets of dorsal ray arise after principal bifurcation 8

7b. External branchlets of dorsal ray arise at or anterior to principal bifurcation 14

8a. Dorsal ray with elongate external branches, vestigial internal branches (Fig. 24 B) . . *Ls. irma*
8b. Dorsal ray with internal branchlets equal to or longer than external branches 9

9a. Spicules > 6 mm 10
9b. Spicules < 6 mm 12

10a. Distal spicule tips straight . . . . . *Ls. flanneryi*
10b. Distal spicule tips curved (Fig. 25 F) 11

11a. Oesophago-intestinal diverticula with 4 prominent lobes (Fig. 25 D). . . . *Ls. petrogale*
11b. Oesophago-intestinal diverticula with tiny pair of posterior lobes (Fig. 23 A) . . *Ls. centralis*

12a. Distal tips of spicules straight . . . . *Ls. thetidis*
12b. Distal tips of spicules curved. 13

13a. Spicule tips symmetrical. . . . . .*Ls. robustus*
13b. Spicule tips asymmetrical, one more robust than other (Fig. 25 B) . . . *Ls. occidentalis*

14a. External branchlets of dorsal ray arise at level of principal division 15
14b. External branchlets of dorsal ray arise anterior to principal division 19

15a. Spicules > 6.0 mm 16
15b. Spicules < 6.0 mm 17

16a. Distal tips of spicules curved (Fig. 23 H); oesophago-intestinal diverticula not elongate (Fig. 23 G) . . . . . .*Ls. camporum*
16b. Distal tips of spicules straight; oesophago-intestinal diverticula elongate (Fig. 24 C) . . . . . .*Ls. dendrolagi*

17a. Oesophago-intestinal diverticula vestigial (Fig. 23 B); submedian lips with paired apical flap-like lobes (Fig. 23 C) . . . . . *Ls. aridus*
17b. Oesophago-intestinal diverticula well developed; submedian lips without paired apical flap-like lobes 18

18a. Oesophago-intestinal diverticula with 3–4 lobes (Fig. 23 M); distal tips of spicules straight (Fig. 23 N) . . . . . .*Ls. communis*
18b. Oesophago-intestinal diverticula with > 6 lobes (Fig. 25 L); distal tips of spicules curved (Fig. 25 M) . . . . . .*Ls. territoriensis*

19a. External branchlets of dorsal ray long, extend posteriorly almost to level of internal branchlets (Fig. 25 A) . . . . . .*Ls. pearsonensis*
19b. External branchlets of dorsal ray not elongate. 20

20a. Submedian lips with paired lobes at distal extremity (Fig. 23 E) . . . . *Ls. bipapillosus*
20b. Submedian lips without paired lobes at distal extremity 21

21a. Distal spicule tips straight 22
21b. Distal spicule tips curved 23

22a. Distance between primary and secondary divisions of dorsal ray equal to length of internal branchlets (Fig. 23 L) . . . . .*Ls. clelandi*
22b. Distance between primary and secondary divisions of dorsal ray twice the length of internal branchlets (Fig. 23 I) . . . . *Ls. bancrofti*

23a. Distal tips of spicules asymmetrical (Fig. 24 A) 24
23b. Distal tips of spicules symmetrical 25

24a. Right spicule more robust, with greater curvature; spicule tip blunt; ala of spicule not reaching tip (Fig. 24 A) . . . . . .*Ls. kungi*
24b. Left spicule with greater curvature; spicule tip sharp; ala of spicule reaching tip (Fig. 25 M) . . . . . .*Ls. turnbulli*

25a. Spicules < 5 mm. . . . . *Ls. godmani*
25b. Spicules < or = 5 mm. 26

26a. Distance between primary and secondary divisions of dorsal ray twice the length of internal branchlets (Fig. 25 G) . . . *Ls. thomasae*
26b. Distance between primary and secondary divisions of dorsal ray equal to length of internal branchlets 27

27a. Oesophago-intestinal diverticula without distinct lobes, not surrounding base of oesophagus (Fig. 23 D) . . . . . .*Ls. australis*
27b. Oesophago-intestinal diverticula with 4 distinct lobes, surrounding base of oesophagus (Fig. 24 J) . . . . . .*Ls. mawsonae*

***Labiosimplex aridus* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *aridus* Smales, 1995, pp. 214–216, figs 179–191.

Labiosimplex aridus: Smales, 2006, pp. 86, 89; Beveridge, 2020c, p. 4; Beveridge, 2020e, p. 204.

Type data: holotype SAM V4203, allotype SAM V4204, paratypes SAM AHC 11640–1.

Type locality: Oban Station via Mount Isa, Qld (21° 14′S 139° 03′E).

Type host: *Osphranter rufus* (Desmarest, 1822).

Other hosts: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: Qld, NSW.

Representative DNA sequence data: ITS1, 2: FR854200.

Diagnostic features (Figs 23 B, C): Males 20–24 mm; females 25–30 mm; submedian lips with paired apical flaps; oesophago-intestinal diverticula very small; external branchlets of dorsal ray arise at principal bifurcation; spicules 5.0–5.8 mm; female tail pointed 0.75–1.00 mm; vagina short, 0.62 mm long; ovejector Y-shaped.

***Labiosimplex australis* (Kung, 1948)**

Labiostrongylus australis Kung, 1948, pp. 102–104, figs 19–24; Skrjabin et al., 1952, p. 178; Popova, 1960, pp. 94–95, fig. 61; Yamaguti, 1961, p. 406.

Labiostrongylus (*Labiosimplex*) *australis*: Smales, 1994, p. 184; 1995, pp. 184–187, figs 1–15.

Labiosimplex australis: Smales, 2002, p. 196; 2006, pp. 86, 98; Chilton et al., 2009b, pp. 229–236; Aussavy et al., 2011, p. 16; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 241.

Labiosimplex quasibancrofti Smales & Chilton, 1997, pp. 196–197, figs 2–16.

Type data: "co-types", BMNH 1949.12.23.76–85.

Type locality: not stated, presumed to be Regent's Park Zoo, London.

Type host: *Morelia spilota* (Lacépède, 1804) (= *Python spilotes* (Lacépède, 1804)) (*lapsus calami*).

Other hosts: *Notamacropus dorsalis* (Gray, 1837); *Notamacropus eugenii* (Desmarest, 1817); *Notamacropus rufogriseus* (Desmarest, 1817); *Thylogale billardierii* (Desmarest, 1822).

Site in host: stomach.

Distribution: Qld, NSW, Vic, SA, Tas.

Representative DNA sequence data: ITS1, 2: FM207449–74.

Diagnostic features (Fig. 23 D): Males 22–26 mm; females 31–38 mm; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise anterior to principal bifurcation; spicules 7.1–9.0 mm; distal spicule tips curved; ala extends to spicule tip; female tail variably pointed 1.14–1.36 mm; vagina elongate, 2.0–2.8 mm long; ovejector J-shaped.

Comments: The type host, *Morelia spilota*, an Australian python, is almost certainly based on a zoo specimen, although this is not stated explicitly in the original description. It is clearly an error and the true host is not a python, but is *N. rufogriseus*, with multiple collections reported from this host species (Smales, 1995). Chilton et al. (2009) conducted a genetic analysis of this species from various hosts, including island populations, but found only minor genetic differentiation within the species.

***Labiosimplex bancrofti* (Johnston & Mawson, 1940)**

Zoniolaimus bancrofti Johnston & Mawson, 1939a, pp. 123–125, figs 1–2; Yamaguti, 1961, p. 403; Skrjabin et al., 1952, p. 172.

Labiostrongylus bancrofti: Kung, 1948, pp. 104, 106; Popova, 1960, p. 95.

Labiostrongylus (*Labiosimplex*) *bancrofti*: Smales, 1994, p. 184; 1995, pp. 187–190, figs 16–30; Beveridge et al., 1989, p. 277; 1998, p. 481; Smales & Chilton, 1997, p. 194.

Labiosimplex bancrofti: Smales, 2006, p. 86, 98, 99.

Type data: holotype, allotype SAM V1541.

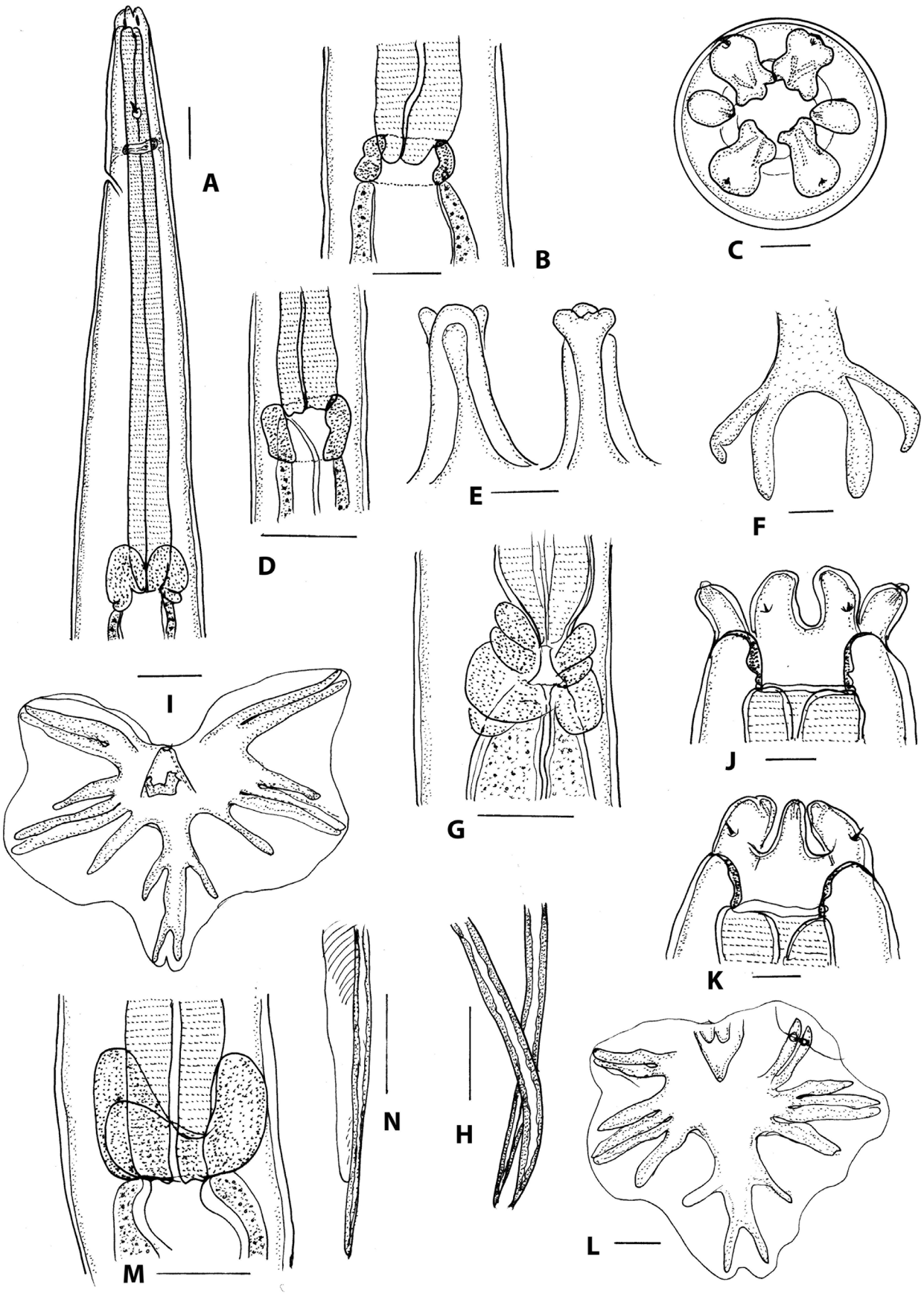
Type locality: Eidsvold, Qld (25° 22′S 151° 07′E).

Type host: *Notamacropus parryi* (Bennett, 1835).

Other hosts: *Notamacropus dorsalis* (Gray, 1837); *Notamacropus parma* (Waterhouse, 1846); *Petrogale assimilis* Ramsay, 1877; *Petrogale herberti* Thomas, 1926;

Fig. 23. Genus *Labiosimplex*. A, *Labiosimplex centralis*, anterior end, lateral view; B, *Labiosimplex aridus*, oesophago-intestinal junction; C, *Ls. aridus*, mouth opening, apical view; D, *Labiosimplex australis*, oesophago-intestinal junction; E, *Labiosimplex bipapillosus*, sub-median lips, external (left) and internal (right) surfaces; F, *Labiosimplex camporum*, dorsal ray, dorsal view; G, *Ls. camporum*, oesophago-intestinal junction; H, *Ls. camporum*, spicule tips; I, *Labiosimplex bancrofti*, bursa, apical view; J, *Labiosimplex clelandi*, buccal capsule, lateral view; K, *Ls. clelandi*, buccal capsule, dorso-ventral view; L, *Ls. clelandi*, bursa, apical view; M, *Labiosimplex communis*, oesophago-intestinal junction; N, *Ls. communis*, spicule tip. (A, from Smales, 2006; B–E, I–N, from Smales, 1995; F–H, from Smales, 2011).

Scale-bars: A, B, D, G, 0.5 mm; C, E, 0.08 mm; F, H, N, 0.05 mm; I, 0.2 mm; J–L 0.1 mm; M, 0.4 mm.


A
B
C
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J
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N

Petrogale inornata Gould, 1842; *Petrogale sharmani* Eldridge & Close, 1992.
Site in host: stomach.
Distribution: eastern Qld.
Representative DNA sequence data: ITS1, 2: FR854201.
Diagnostic features (Fig. 23 I): Males 19–45 mm; females 50–60 mm; oesophago-intestinal diverticula well developed, anterior lobe much larger than posterior lobe; external branchlets of dorsal ray arise well anterior to principal bifurcation; spicules 4.40–6.85 mm; distal spicule tips straight; ala terminates anterior to spicule tip; female tail conical with terminal knob, 1.02–1.36 mm; vagina sinuous, 1.7–2.7 mm long; ovejector J-shaped.
Comments: Based on current collection data, *N. parryi* appears to be the principal host of this species, with limited occurrences in sympatric species in eastern Queensland (Beveridge et al., 1989, 1998).

***Labiosimplex bipapillosus* (Johnston & Mawson, 1939)**
Zoniolaimus bipapillosus Johnston & Mawson, 1939a, p. 125, figs 3–5; 1940c, p. 364; Skrjabin et al., 1952, p. 172; Yamaguti, 1961, p. 403.
Labiostrongylus bipapillosus: Kung, 1948, pp. 104, 106; Popova, 1960, p. 96; Arundel et al., 1977, p. 142; Beveridge & Arundel, 1979, pp. 72, 74; Arundel et al., 1990, pp. 42, 49; Beveridge et al., 1998, p. 481.
Labiostrongylus (*Labiosimplex*) *bipapillosus*: Smales, 1995, pp. 190–193, figs 31–48.
Labiosimplex bipapillosus: Smales, 2006, p. 99; Aussavy et al., 2011, p. 14; Cripps et al., 2015, p. 168.
Type data: holotype, allotype SAM V1542.
Type locality: Upper Dawson Valley, Qld (32° 54′S 149° 50′E).
Type host: *Macropus giganteus* Shaw,1790 (as *Macropus major* Shaw, 1800).
Other hosts: *Macropus fuliginosus* (Desmarest, 1817).
Site in host: stomach.
Distribution: eastern Qld, NSW, ACT, Vic.
Representative DNA sequence data: ITS1, 2: FR854202.
Diagnostic features (Fig. 23 E): Males 29–47 mm; females 40–65 mm; submedian lips with paired distal processes; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise anterior to principal bifurcation; spicules 4.20–5.75 mm; distal spicule tips curved; ala terminates anterior to spicule tip; female tail conical, 1.0–1.6 mm; vagina sinuous, 0.9 mm long; ovejector J-shaped.
Comments: *Labiosimplex bipapillosus* is primarily a parasite of *Mac. giganteus* and is more common in northern regions of the host's distribution (Beveridge et al., 1998). The single record from *Mac. fuliginosus* (in Smales, 1995) was in an area of sympatry between the two species of kangaroos. However, Aussavy et al. (2011) in another area of sympatry found *L. bipapillosus* only in *Mac. giganteus*. The single record of *L. bipapillosus* in *O. robustus* is dubious and may be due to an error in host identification (Smales, 1995). It has not been found in *O. robustus* subsequently (Beveridge, 2020c).

***Labiosimplex camporum* Smales, 2011**
Labiosimplex camporum Smales, 2011, pp. 187–189, figs 18–33; Beveridge, 2020c, p. 4, 2020e, p. 204.
Type data: holotype WAM V7706, allotype WAM V7707, paratypes WAM V7708, SAM AHC 45446.
Type locality: Menzies, WA (29° 41′S 121° 02′E).
Type host: *Osphranter rufus* (Desmarest, 1822).
Other hosts: *Osphranter robustus* (Gould, 1840).
Site in host: stomach.
Distribution: WA (Pilbara Division).
Diagnostic features (Figs 23 F–H): Males 38–60 mm; females 55–120 mm; oesophago-intestinal diverticula prominently 4-lobed; external branchlets of dorsal ray arise at principal bifurcation; spicules 6.20–6.97 mm; distal spicule tips slightly curved; ala extending to spicule tip; female tail conical, 0.94–1.6 mm; vagina sinuous, 1.36–2.55 mm long; ovejector J-shaped.

***Labiosimplex centralis* Smales, 2006**
Labiosimplex centralis Smales, 2006, pp. 89–92, 100, figs 19–34.
Labiostrongylus (*Labiosimplex* sp.): Smales, 1995, p. 237.
Type data: holotype SAM AHC 32898, allotype SAM AHC 32899, paratypes SAM AHC 2949.
Type locality: Mount Liebig, NT (26° 16′S 131° 16′E).
Type host: *Petrogale lateralis* Gould, 1840 (MacDonnell Ranges race).
Site in host: stomach.
Distribution: NT (Central Australia), northern SA.
Diagnostic features (Fig. 23 A): Males 30–50 mm; females 47–65 mm; oesophago-intestinal diverticula prominently 4-lobed; external branchlets of dorsal ray arise posterior to principal bifurcation; spicules 6.46–8.08 mm; distal spicule tips straight; ala terminates anterior to spicule tip; female tail conical, 0.85–1.45 mm; vagina straight, 1.36–3.06 mm long; ovejector J-shaped.

***Labiosimplex clelandi* (Johnston & Mawson, 1939)**

Zoniolaimus clelandi Johnston & Mawson, 1939b, pp. 521–522, figs 23–25; 1939d, p. 308; Skrjabin et al., 1952; p. 172; Yamaguti, 1961, p. 403.

Labiostrongylus clelandi: Kung, 1948, pp. 104, 106; Popova, 1960, p.96, fig. 62; Beveridge et al., 1985, p. 378.

Labiostrongylus (*Labiosimplex*) *clelandi*: Smales, 1994, p. 184; Smales, 1995, pp. 193–195, figs 49–61.

Labiosimplex clelandi: Smales, 2006, p. 86, 100; Beveridge, 2016, p. 211; Spratt et al., 2017, p. 242.

Zoniolaimus ualabatus Johnston & Mawson, 1939b, pp. 521–522, fig. 26; 1939d, p. 308; Skrjabin et al., 1952, p.174; Yamaguti, 1961, p. 404.

Labiostrongylus ualabatus: Kung, 1948, pp. 104, 106; Popova, 1960, p.104, fig. 68.

Type data: holotype, allotype SAM V1686; paratypes SAM V1616, SAM AHC 2943, 3086.

Type locality: Lower Hawkesbury River, NSW (33° 30′S 151° 10′E).

Type host: *Wallabia bicolor* (Desmarest, 1804) (as *Macropus ualabatus* (Lesson, 1827)).

Other hosts: *Notamacropus rufogriseus* (Desmarest, 1817).

Site in host: stomach.

Distribution: NSW, Vic.

Representative DNA sequence data: ITS1, 2: FR854203.

Diagnostic features (Figs 23 J–L): Males 19–23 mm; females 29–33 mm; oesophago-intestinal diverticula prominently 4-lobed; external branchlets of dorsal ray arise well anterior to principal bifurcation; spicules 5.4–6.1 mm; distal spicule tips straight; ala almost reaching spicule tip; female tail conical, 0.90–1.20 mm, with or without terminal knob; vagina sinuous, 1.40–2.80 mm long; ovejector J-shaped.

Comments: *Labiosimplex clelandi* occurs more commonly in the southern part of the geographical range of its host, *Wal. bicolor* (Beveridge, 2016). The single record from *N. rufogriseus* from Tasmania (Smales, 2006, p. 86) is of interest as the principal host, *Wal. bicolor*, does not occur in Tasmania. An immature male and female *Labiosimplex* cf *clelandi* were collected from *N. parma* from Narara in NSW in 1909 (SAM AHC 3896). The limited range of the extant parma wallaby population makes it unlikely that the additional material needed to provide an adequate description will become available (Smales, 1995, p. 237).

***Labiosimplex communis* (Johnston & Mawson, 1939)**

Zoniolaimus communis Johnston & Mawson, 1939a, pp. 125–126, figs 6–7; 1939b, p. 522; 1939d, p. 308; Skrjabin et al., p. 174; Yamaguti, 1961, p. 403.

Labiostrongylus communis: Kung, 1948, pp. 104, 106; Popova, 1960, p. 97; Beveridge et al., 1985, p. 378; 1998, p. 481.

Labiostrongylus (*Labiosimplex*) *communis*: Smales, 1994, p. 185; 1995, pp. 195–198, figs 62–76.

Labiosimplex communis: Smales, 2006, p. 98, 100; Beveridge, 2016, p. 211.

Type data: holotype, allotype SAM V1543.

Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).

Type host: *Wallabia bicolor* (Desmarest, 1804) (as *Macropus ualabatus* (Lesson, 1827)).

Other hosts: *Lagorchestes hirsutus* Gould, 1844; *Notamacropus dorsalis* (Gray, 1837); *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: Qld, NSW.

Representative DNA sequence data: ITS1, 2: FR854204.

Diagnostic features (Figs 23 M, N): Males 14–24 mm; females 24–29 mm; oesophago-intestinal diverticula prominently 4-lobed; external branchlets of dorsal ray arise at principal bifurcation; spicules 4.35–5.20 mm; distal spicule tips straight; ala terminates anterior to spicule tip; female tail conical, 0.80–1.05 mm; vagina sinuous, 0.92–1.30 mm long; ovejector J-shaped.

Comments: *Labiosimplex communis* is a frequent parasite of *Wal. bicolor* in Queensland and occurs commonly there also in *N. dorsalis* (Beveridge et al., 1998; Beveridge, 2016). There is a single record of its occurrence in *Thyl. stigmatica* in northern New South Wales in an area where this host is sympatric with both *Wal. bicolor* and *N. dorsalis*.

Johnston & Mawson (1940a) reported *Ls. communis* from *Lagorchetes hirsutus*. The specimens, now in very poor condition, referred to as *Labiostronylus (Labiosimplex)* sp. 3 by Smales (1995, p.237) (SAM AHC 4965) most closely resemble *Ls. australis,* although there are some differences in spicule length, the shape of the gubernaculum and the appendages of the genital cone. Such differences are sufficient to suggest that this material represents an undescribed species. The likelihood of obtaining additional material to complete a description is remote, given that *L. hirsutus,* the rufous hare wallaby, is now largely restricted to Bernier and Dorré Islands off the western Australian coast (Smales, 1995)

***Labiosimplex dendrolagi* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *dendrolagi* Smales, 1995, pp. 226–228, figs 252–265.

Labiosimplex dendrolagi: Smales, 2006, p. 98; Shima et al., 2019, p. 62.

Type data: holotype SAM V4193, allotype SAM V4194, paratypes SAM AHC 10861–4.

Type locality: Atherton, Qld (17° 16′S 145° 29′E).

Type host: *Dendrolagus lumholtzi* Collett, 1884.

Other hosts: *Dendrolagus bennettianus* De Vis, 1887.

Site in host: stomach.

Distribution: north-eastern Qld.

Representative DNA sequence data: ITS1, 2: FR854205; MN864140–1 (unpublished sequences, morphological voucher specimens SAM AHC 48748, 48753).

Diagnostic features (Fig. 24 C): Males 24–28 mm; females 32–41 mm; oesophago-intestinal diverticula prominently elongated anteriorly; external branchlets of dorsal ray arise at principal bifurcation; spicules 6.0–9.0 mm; distal spicule tips straight; ala almost reaches spicule tip; female tail conical, 0.95–1.43 mm; vagina 2.2–3.6 mm long; ovejector J-shaped.

Comments: The sequence data cited are from nematodes from the two species of *Dendrolagus* indicating the conspecificity of the nematodes.

***Labiosimplex flanneryi* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *flanneryi* Smales, 1995, pp. 216–219, figs 192–207.

Labiostrongylus flanneryi: Griffith et al., 2000, p. 310.

Labiosimplex flanneryi: Smales, 2006, pp.

Type data: holotype, SAM V4187, allotype SAM V4188, paratypes SAM AHC 11827.

Type locality: Mount Albert Edward, Neum Basin, PNG (8° 24′S 147° 24′E).

Type host: *Thylogale calabyi* Flannery, 1992.

Other hosts: *Petrogale assimilis* Ramsay, 1877; *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: PNG, north-eastern Qld.

Representative DNA sequence data: ITS1, 2: FR854225–6

Diagnostic features: Males 13–17 mm; females 16–32 mm; oesophago-intestinal diverticula very small, bilobed; external branchlets of dorsal ray arise posterior to principal bifurcation; spicules 7.95–9.95 mm; distal spicule tips straight; ala terminating anterior to spicule tip; female tail conical, 0.83–1.25 mm; vagina sinuous 2.0–4.0 mm long; ovejector J-shaped.

***Labiosimplex godmani* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *godmani* Smales, 1995, pp. 231–233, figs 284–298.

Labiosimplex godmani: Smales, 2006, p. 99.

Type data: holotype SAM V4197, allotype SAM V4198, paratypes SAM AHC 11150, 11850, 11872, 12863.

Type locality: Mount Elephant, Cooktown, Qld (16° 27′S 144° 56′E).

Type host: *Petrogale godmani* Thomas, 1923.

Other hosts: *Petrogale coenensis* Eldridge & Close, 1992.

Site in host: stomach.

Distribution: north-eastern Qld.

Diagnostic features: Males 28–32 mm; females 30–37 mm; oesophago-intestinal diverticula prominent; external branchlets of dorsal ray arise well posterior to principal bifurcation; spicules 3.4–4.4 mm; distal spicule tips curved; ala terminating at spicule tip; female tail conical, 0.65–0.95 mm with terminal knob; vagina straight 0.55–0.75 mm long; ovejector J-shaped.

***Labiosimplex irma* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *irma* Smales, 1995, pp. 222–224, figs 222–238; 2011, p. 184.

Labiosimplex irma: Smales, 2006, p. 99.

Type data: holotype SAM V4191, allotype SAM V4192, paratypes SAM AHC 5979, 11597.

Type locality: Jandakot, WA (32° 07′S 115° 50 ′E).

Type host: *Notamacropus irma* (Jourdan, 1837).

Site in host: stomach.

Distribution: south-western WA.

Representative DNA sequence data: ITS1, 2: FR854206.

Diagnostic features (Fig. 24 B): Males 29–33 mm; females 34–38 mm; oesophago-intestinal diverticula prominent; stem of dorsal ray very short; branches highly arcuate; external branchlets of dorsal ray prominent, reach margin of bursa; internal branchlets vestigial; spicules 4.68–5.75 mm; distal spicule straight; ala terminating at spicule tip; female tail conical, blunt, 0.95–1.28 mm; vagina sinuous 1.50–2.00 mm long; ovejector J-shaped.

***Labiosimplex kungi* (Mawson, 1955)**

Labiostrongylus kungi Mawson, 1995, pp. 3–4, figs 7–9; Arundel et al., 1977, p. 142; Beveridge & Arundel, 1979, pp. 72, 74; Arundel et al., 1990, pp. 42, 49.

Labiostrongylus (*Labiosimplex*) *kungi*: Smales, 1994, p. 185; 1995, pp. 198–200, figs 77–93.

Labiosimplex kungi: Smales, 2006, p. 99; 2011, p. 184; Aussavy et al., 2011, pp. 14, 15; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240.

Type data: "types" SAM AHC 12409 (no holotype designated).
Type locality: New South Wales.
Type host: *Macropus giganteus* Shaw, 1790 (as *Macropus major* Shaw, 1800).
Other hosts: *Macropus fuliginosus* (Desmarest, 1817).
Site in host: stomach.
Distribution: NSW, Vic, SA, south-western WA.
Representative DNA sequence data: ITS1, 2: FR854207.
Diagnostic features (Fig. 24 A): Males 41–48 mm; females 55–70 mm; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise anterior to principal bifurcation; spicules 4.75–5.90 mm; distal spicules curved, asymmetrical, right spicule thicker than left; ala terminating anterior to spicule tip; female tail conical, 0.8–1.20 mm; vagina short, straight, 1.50–2.00 mm long; ovejector J–shaped.

***Labiosimplex laterilabellosus* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *laterilabellosus* Smales, 1995, 234–236, figs 299–316.
Labiosimplex laterilabellosus: Smales, 2006, p. 99; Aussavy et al, 2011, p. 15; Spratt et al., 2017, p. 244.
Type data: holotype SAM V4209, allotype SAM V4210, paratypes SAM AHC 10171.
Type locality: You Yang Range, Vic (37° 57'S 144° 26'E).
Type host: *Macropus giganteus* Shaw, 1790.
Other hosts: *Macropus fuliginosus* (Desmarest, 1817).
Site in host: stomach.
Distribution: NSW, Vic, SA.
Diagnostic features (Figs 24 G, H): Males 44–47 mm; females 65–72 mm; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise well anterior to principal bifurcation; spicules 13.4 –15.6 mm; spicule tips straight; ala terminating anterior to spicule tip; female tail conical, 1.20–1.46 mm with knobbed tip; vagina sinuous, 4.00–5.04 mm long; ovejector J-shaped.

***Labiosimplex longispicularis* Wood, 1929**

Labiostrongylus longispicularis Wood, 1929a, pp. 550–551; Johnston & Mawson, 1938, pp. 268–269, figs 15–17; Kung, 1948, pp. 104, 106; Popova, 1960, pp. 100–101, fig. 65; Yamaguti, 1961, p. 406; Mykytowycz, 1964, pp. 677, 682, 683, 686; Dudzinski & Mykytowycz, 1965, pp. 543–550; Mykytowycz & Dudzinski, 1965, pp. 527–541; Arundel et al., 1979, pp. 365–369, 375.
Zoniolaimus longispicularis: Johnston & Mawson, 1939a, p. 123; 1940c, p. 364; Skrjabin et al., 1952, p. 174.
Labiostrongylus (*Labiosimplex*) *longispicularis*: Smales, 1994, p. 184; 1995, pp. 201–204, figs 94–108.
Labiosimplex longispicularis: Smales, 2006, p. 99; 2011, p. 184; Beveridge, 2020c, p. 4, 2020e, p. 204.
Type data: not known.
Type locality: not stated, probably Western Australia based on Wood (1931).
Type host: *Osphranter robustus woodwardi* (Thomas, 1901).
Other hosts: *Osphranter rufus* (Desmarest, 1822) (see comments).
Site in host: stomach.
Distribution: Qld, NSW, SA, WA.
Representative DNA sequence data: ITS1, 2: FR854208–10; cox1: KJ851993–6; 18S, 28S: KJ851987–90, KJ736388–91.
Diagnostic features (Figs 24 D–F): Males 48–50 mm; females 67–79 mm; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise well anterior to principal bifurcation; spicules 10.5–14.0 mm; spicule tips curved, asymmetrical, right spicule tip more recurved than left; ala terminating anterior to spicule tip; female tail conical, 1.60–1.80 mm with knobbed tip; vagina sinuous, 2.6–4.0 mm long; ovejector J–shaped.
Comments: The principal hosts of this species are *O. robustus* and *O. rufus* (Smales, 1995). However, the additional host species are difficult to determine as a number of the early identifications of *Ls. longispicularis* in other host species have since been described as independent species (Smales, 1995). Spratt & Beveridge (2016) listed *N. dorsalis* and *Pet. xanthopus* as dubious host records. However, the records of this species in *N. eugenii* (Smales & Mawson, 1978a) and *N. rufogriseus* (Munday & Green, 1972) remain to be verified.

The type host of *Ls. longispicularis* appears to have been the source of some confusion. In the original description, Wood (1929a, p. 205) stated that the host was "....a small species of red kangaroo (*Macropus woodwardi*) ...", now *Osphranter robustus woodwardi*. In describing the same species from *O. r. erubescens* in South Australia, Johnston & Mawson (1938, p. 268) claimed that the type locality was the Murchison region of Western Australia. However, as Smales (1995, p. 202) has pointed out, *O. r. erubescens* but not *O. r. woodwardi* occurs in this region. It appears that Johnston & Mawson (1938) were alluding to a second paper by Wood (1931) based on the same collection of nematodes, in which (p. 209) he mentions "Western Australia" for the first time. Johnston & Mawson (1938) probably relied on Iredale & Troughton (1934) for host taxonomy and on p. 51,

they list *Macropus robustus cervinus* Thomas, from the Murchison District of WA, with *M. r. erubescens* Schwartz as a synonym. This is apparently the only mention of the "Murchison district" in papers on the distribution of *O. robustus*. Troughton (1941, p. 183) refers to *Osphranter cervinus* as the "western red wallaroo" and includes *O. cervinus woodwardi* as a subspecies. The complex taxonomy of the host and the incorrect assumption that the Murchison district was the type locality by Johnston & Mawson (1938) may have led to this confusion. However, current records indicate that it occurs in both *O. r. erubescens* and in *O. r. robustus*, but there are no confirmatory collections from *O. r. woodwardi* (Beveridge, 2020c).

Smales (1995, p. 201) stated that a male holotype was present at the British Museum. However, collections records there show no evidence of such a specimen (E. Harris, personal communication).

***Labiosimplex major* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *major* Smales, 1995, pp. 209–212, figs 142–160.

Labiosimplex major: Smales, 2006, p. 99; Aussavy et al., 2011, pp. 14, 15; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240.

Type data: holotype SAM V4207, allotype SAM V4208, paratypes SAM AHC 5428, 8440, 8475, 9760, 9790, 9791, 9836, 9869, 9874, 10672, 18413, 18415, 18418, 18420, 18422–4, 19206.

Type locality: Pine Plains Station via Patchewollock, Vic. (35° 26′S 141° 6′E).

Type host: *Macropus fuliginosus* (Desmarest, 1817).

Other hosts: *Macropus giganteus* Shaw, 1790.

Site in host: stomach.

Distribution: NSW, Vic, SA, Tas.

Representative DNA sequence data: ITS1, 2: FR854211.

Diagnostic features (Fig. 24 I): Males 45–56 mm; females 62–70 mm; oesophago-intestinal diverticula prominent; external branchlets of dorsal ray arise at principal bifurcation with some variation, either slightly anterior or slightly posterior to bifurcation; spicules 12.0–15.6 mm; spicule tips straight; ala extending to spicule tip; female tail conical, 1.30–1.76 mm; vagina sinuous, 3.0–4.0 mm long; ovejector J-shaped.

***Labiosimplex mawsonae* Smales, 2011**

Labiosimplex mawsonae Smales, 2011, pp. 184–186, figs 1–17.

Type data: holotype WAM V7711, allotype WAM V7712, paratypes WAM V7713, SAM AHC 45790.

Type locality: 80 km N of Williams, WA (32° 21′S 116° 52′E).

Type host: *Notamacropus irma* (Jourdan, 1837).

Site in host: stomach.

Distribution: south-western WA.

Diagnostic features (Fig. 24 J): Males 22–27 mm; females 27–33 mm; oesophago-intestinal diverticula large; external branchlets of dorsal ray arise immediately anterior to principal bifurcation; spicules 7.82–9.35 mm; spicule tips prominently recurved; ala extending to spicule tip; female tail conical, 1.02–1.28 mm; vagina sinuous, 2.38–3.06 mm long; ovejector J–shaped.

***Labiosimplex occidentalis* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *occidentalis* Smales, 1995, pp. 212–214, figs 161–178; 2011, p. 184.

Labiosimplex occidentalis: Smales, 2006, p. 99.

Type data: holotype SAM V4201, allotype SAM V4202, paratypes SAM AHC 8681.

Type locality: Dungunna via Cranbrook, WA (34° 17′S 117° 33′E).

Type host: *Macropus fuliginosus* (Desmarest, 1817).

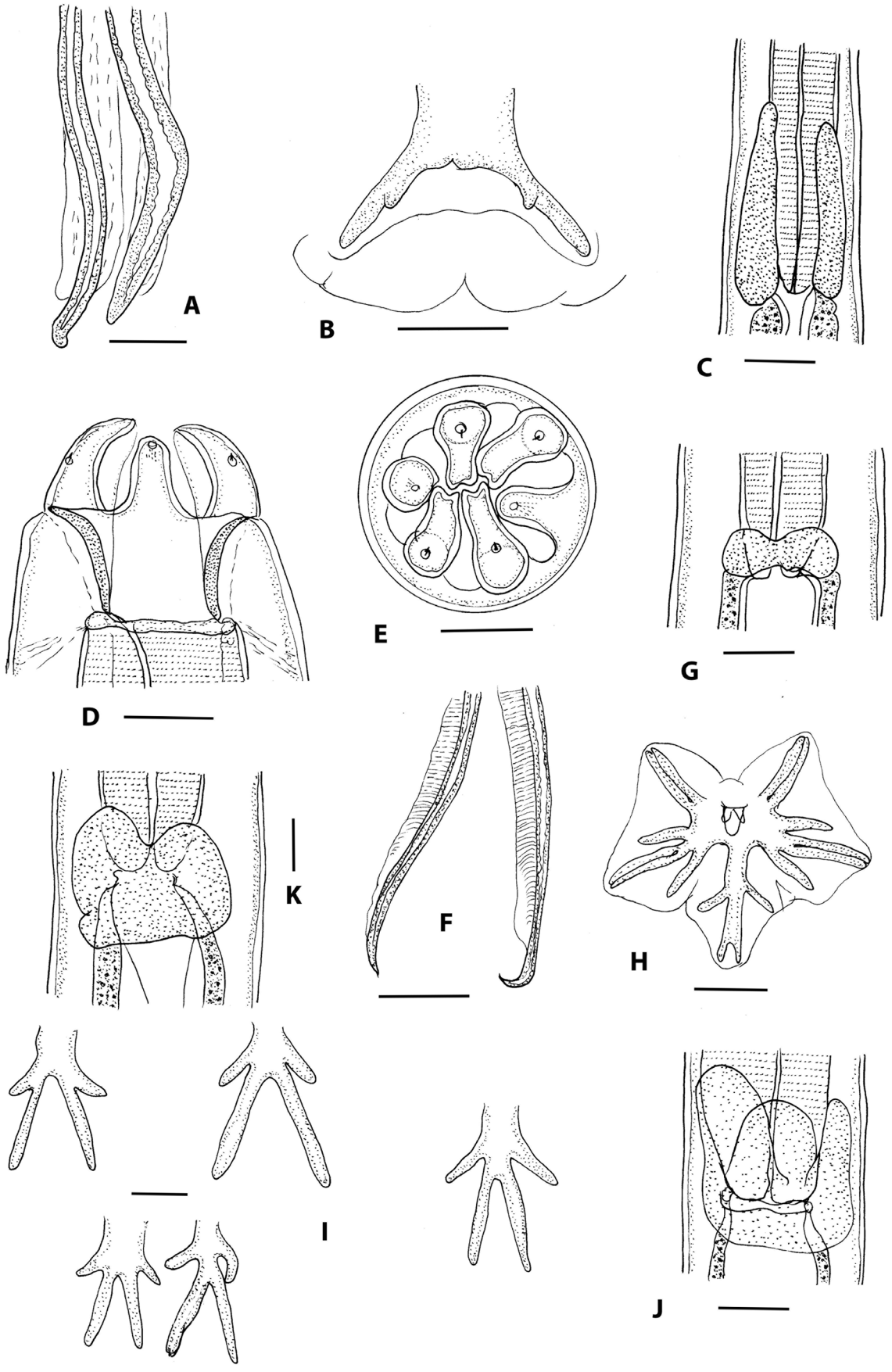
Site in host: stomach.

Distribution: south-western WA.

Diagnostic features (Figs 25 B, C): Males 45–51 mm; females 55–67 mm; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise immediately posterior to principal bifurcation; spicules 3.92–4.32 mm; spicule tips curved, asymmetrical; ala extending to spicule tip; female tail conical, 1.28–1.76 mm, usually with spike; vagina short, 0.72–1.12 mm long; ovejector J-shaped.

Fig. 24. Genus *Labiosimplex*. A, *Labiosimplex kungi*, spicule tips; B, *Labiosimplex irma*, dorsal ray of bursa, dorsal view; C, *Labiosimplex dendrolagi*, oesophago-intestinal junction; D, *Labiosimplex longispicularis*, buccal casule, dorso-ventral view; E, *Ls. longispicularis*, mouth opening, apical view; F, *Ls. longispicularis*, spicule tips; G, *Labiosimplex laterilabellosus*, oesophago-intestinal junction; H, *Ls. laterilabellosus*, bursa, apical view; I, *Labiosimplex major*, variation in the shape of the dorsal ray; J, *Labiosimplex mawsonae*, oesophago-intestinal junction; K, *Ls. major,* oesophago-intestinal junction. (A–C, G–I, K, from Smales, 1995; D–F, original; J from Smales, 2011).

Scale-bars: A, C, G, 0.5 mm; B, 0.16 mm; D–F, 0.1 mm; H, 0.4 mm; I–K, 0.2 mm.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***Labiosimplex papuensis* Purwaningsih & Smales, 2011**

Labiosimplex papuensis Purwaningsih & Smales, 2011, pp. 125–127, figs 1–13.

Type data: holotype, allotype MZB Na 489, paratypes MZB Na 490.

Type locality: Teluk Sagawin District, Salawati Island, Western New Guinea (1º 06'S 130º 51'E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea .

Diagnostic features: Males 7.4–9.4 mm; females 7.7–67 mm; lips triangular; oesophago-intestinal diverticula prominent; external branchlets of dorsal ray arise posterior to principal bifurcation; spicules 2.98–8.8 mm; spicule tips curved; ala extending almost to spicule tip; female tail conical, 0.51–0.67 mm; vagina straight, 0.77–1.10 mm long; ovejector J-shaped.

***Labiosimplex pearsonensis* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *pearsonensis* Smales, 1995, pp. 229–231, figs 266–283.

Labiosimplex pearsonensis: Smales, 2006, p. 99.

Type data: holotype SAM V4205, allotype SAM V4206, paratypes SAM AHC 1852, 1853, 1944, 2918, 5254.

Type locality: Pearson Island, SA (33° 58'S 134° 17'S).

Type host: *Petrogale lateralis pearsoni* Thomas, 1922.

Site in host: stomach.

Distribution: SA (Pearson Island).

Diagnostic features (Fig. 25 A): Males 20–33 mm; females 22–30 mm; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise well anterior to principal bifurcation, very long, arcuate, extending almost to level of tips of internal branchlets; spicules 9.70–12.1 mm; spicule tips curved; ala ending anterior to spicule tip; female tail conical, 0.83–1.25 mm; vagina 2.00–2.50 mm long; ovejector J-shaped.

***Labiosimplex petrogale* (Johnston & Mawson, 1938)**

Labiostrongylus petrogale Johnston & Mawson, 1938, pp. 270–271, figs 21–22; Kung, 1948, pp. 104, 106; Skrjabin et al., 1952, p. 162; Popova, 1960, pp. 103–104, fig. 67; Yamaguti, 1961, p. 406.

Zoniolaimus petrogale: Johnston & Mawson, 1939a, p. 123.

Labiostrongylus (*Labiosimplex*) *petrogale*: Smales, 1995, pp. 204–205, figs 109–125.

Labiosimplex petrogale: Smales, 2006, p. 99.

Type data: holotype, allotype SAM V1376.

Type locality: Mount Liebig, NT (23° 19'S 131° 22'E).

Type host: *Petrogale lateralis* Gould,1840 (MacDonnell Ranges race).

Site in host: stomach.

Distribution: NT (Central Australia).

Diagnostic features (Figs 25 D–F): Male 37 mm; female 55 mm; oesophago-intestinal diverticula large; trunk of dorsal ray elongate, principal bifurcation occurring close to posterior end; external branchlets of dorsal ray arise posterior to principal bifurcation; external and internal brnachlets very short; spicules 7.25 mm; spicule tips curved; ala ending anterior to spicule tip; female tail conical, 0.72 mm with terminal knob; vagina 1.7 mm long; ovejector J-shaped.

***Labiosimplex redmondi* Smales, 1982**

Labiostrongylus redmondi Smales, 1982a, pp. 365–367, figs 11–21.

Labiostrongylus (*Labiosimplex*) *redmondi*: Smales, 1995, pp. 205–206.

Labiosimplex redmondi: Smales, 2006, p. 98.

Type data: holotype BMNH 1981.4543, allotype BMNH 1981.4544, paratypes BMNH 1981. 4545–4550, SAM AHC 8985.

Type locality: Middle Strickland, PNG (7° 1'S 142° 12'E).

Type host: *Dorcopsis luctuosa* (D'Albertis, 1874) (as *D. veterum* Lesson, 1827).

Other hosts: *Dorcopsis hageni* Heller, 1897.

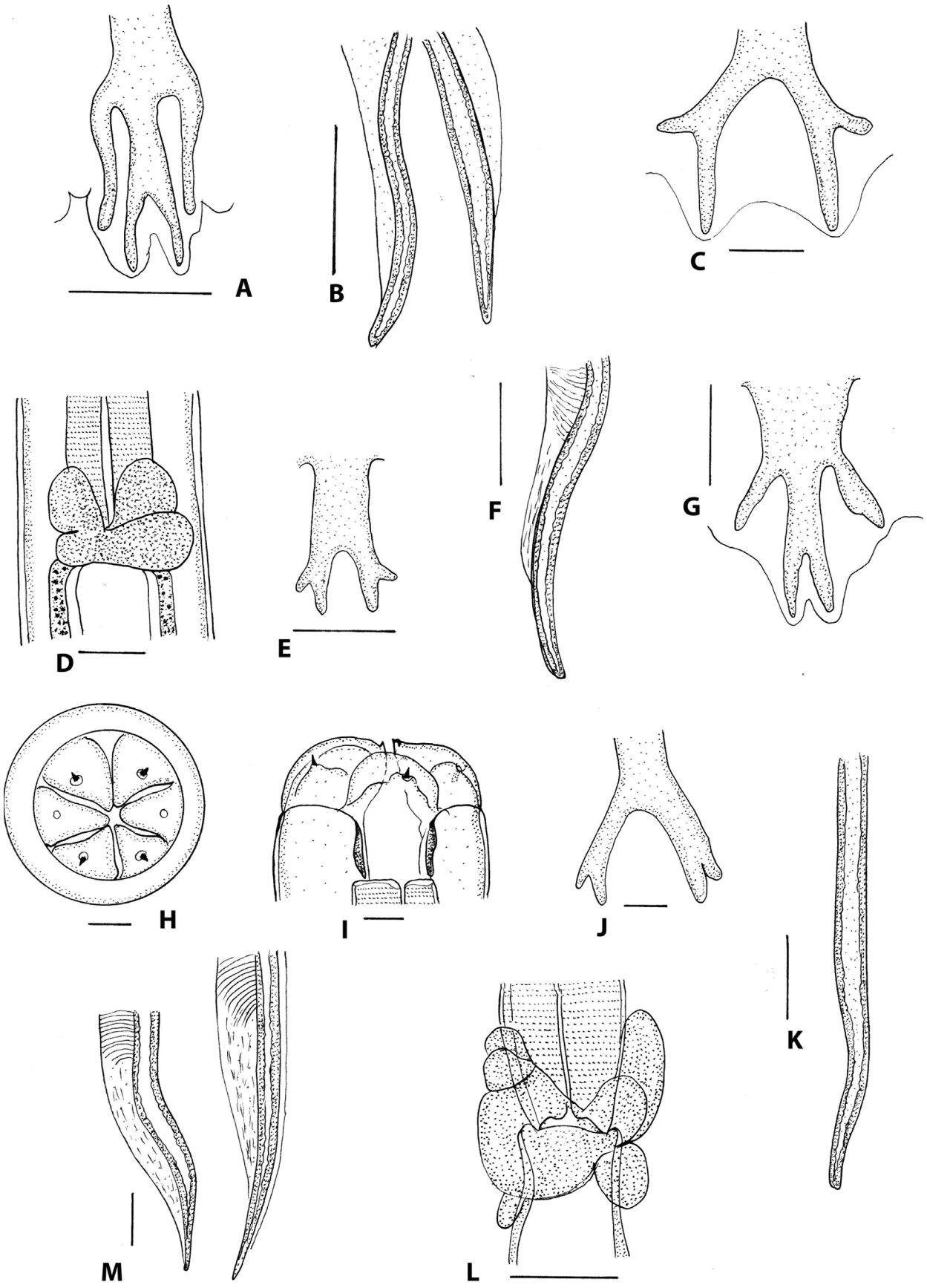
Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 25 H, I): Males 24–29 mm; females 35–44 mm; lips triangular; oesophago-intestinal diverticula prominent; external branchlets of dorsal ray arise posterior to principal bifurcation; spicules 5.0–7.2 mm; ala extending almost to spicule tip; female tail conical, 1.29–1.77 mm; vagina 2.6–3.4 mm long; ovejector J–shaped.

Fig. 25. Genus *Labiosimplex*. A, *Labiosimplex pearsonensis*, dorsal lobe of bursa, dorsal view; B, *Labiosimplex occidentalis*, spicule tips; C, *Ls. occidentalis*, dorsal ray of bursa, dorsal view; D, *Labiosimplex petrogale*, oesophago-intestinal junction; E, *Ls. petrogale*, dorsal ray of bursa, dorsal view; F, *Ls. petrogale*, spicule tip; G, *Labiosimplex thomasae*, dorsal ray of bursa, dorsal view; H, *Labiosimplex redmondi*, mouth opening, apical view; I, *Ls. redmondi,* buccal capsule, oblique view; J, *Ls. redmondi,* dorsal ray of bursa, dorsal view; K, *Labiosimplex territoriensis*, spicule tip; L, *Ls. territoriensis*, oesophago-intestinal junction; M, *Labiosimplex turnbulli*, spicule tips. (A–G, from Smales, 1995; H–J from Smales, 1982a; K, L, from Smales, 2006; M, from Smales & Chilton, 1997).

Scale-bars: A, E, G, L, 0.2 mm; B, C, F, H, J, 0.1 mm; D, 1.0 mm; I, K, 0.05 mm; M, 0.025 mm.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***Labiosimplex robustus* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *robustus* Smales, 1995, 207–209, figs 126–141; Beveridge et al., 1998, p. 482.
Labiosimplex robustus: Smales, 2006, p. 99; Beveridge, 2020c, p. 4.
Type data: holotype SAM V4195, allotype SAM V4196, paratypes SAM AHC 10525–6.
Type locality: Kingstown, NSW (30° 30′S 151° 20′E).
Type host: *Osphranter robustus* (Gould, 1840).
Site in host: stomach.
Distribution: Qld, NSW.
Representative DNA sequence data: ITS1, 2: FR854212.
Diagnostic features: Males 40–49 mm; females 50–82 mm; oesophago-intestinal diverticula prominent; external branchlets of dorsal ray arise posterior to principal bifurcation; spicules 4.3–5.5 mm; spicule tips curved; ala not extending to spicule tip; female tail conical, 1.40–2.20 mm; vagina sinuous, 1.0–1.4 mm long; ovejector J-shaped.

***Labiosimplex territoriensis* Smales, 2006**

Labiosimplex territoriensis Smales, 2006, pp. 92–94, 98, figs 35–51.
Type data: holotype SAM AHC 32894, allotype SAM AHC 32895, paratypes SAM AHC 6425.
Type locality: Jabiluka, NT (12° 20′S 132° 52′E).
Type host: *Osphranter antilopinus* (Gould, 1842).
Site in host: stomach.
Distribution: NT (Top End).
Diagnostic features (Figs 25 K, L): Males 35–50 mm; females 43–57 mm; oesophago-intestinal diverticula prominent with multiple lobes; external branchlets of dorsal ray arise at principal bifurcation; spicules 3.4–4.2 mm; spicule tips curved; female tail conical, 0.94–1.41 mm, with terminal knob; vagina sinuous, 0.65–0.85 mm long; ovejector J-shaped.

***Labiosimplex thetidis* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *thetidis* Smales, 1995, pp. 219–221, figs 208–221.
Labiostrongylus thetidis: Griffith et al., 2000, p. 310.
Labiosimplex thetidis: Smales, 2006, p. 100.
Type data: holotype SAM V4199, allotype SAM V4200, paratypes SAM AHC 6917, 10449, 10570.
Type locality: Emuvale, Qld. (28° 13′S 152° 14′E).
Type host: *Thylogale thetis* (Lesson, 1827).
Other hosts: *Thylogale stigmatica* (Gould, 1860); *Onychogalea unguifera* (Gould, 1840).
Site in host: stomach.
Distribution: eastern Qld; north-eastern NSW.
Representative DNA sequence data: ITS1, 2: FR854213.
Diagnostic features: Males 18–23 mm; females 24–30 mm; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise posterior to principal bifurcation; spicules 3.5–5.0 mm; spicule tips straight; ala extending to spicule tip; female tail conical, 0.85–1.09 mm; vagina sinuous, 1.4 mm long; ovejector J-shaped.

***Labiosimplex thomasae* Smales, 1995**

Labiostrongylus (*Labiosimplex*) *thomasae* Smales, 1995, pp. 224–226, figs 239–251.
Labiosimplex thomasae: Smales, 2006, p. 98.
Type data: holotype SAM V4189, allotype SAM V4190, paratypes SAM AHC 23049.
Type locality: Garden Island, WA (32° 12′S 115° 40′E).
Type host: *Notamacropus eugenii* (Desmarest, 1817).
Site in host: stomach.
Distribution: south-western WA.
Representative DNA sequence data: ITS1, 2: FR854214.
Diagnostic features: Males 20–22 mm; females 24–26 mm; oesophago-intestinal diverticula small; external branchlets of dorsal ray arise well anterior to principal bifurcation; spicules 9.0–9.9 mm; spicule tips curved; ala not extending to spicule tip; female tail conical, 0.90–1.01 mm; vagina sinuous, 1.40–1.42 mm long; ovejector J-shaped.

***Labiosimplex turnbulli* Smales & Chilton, 1997**

Labiostrongylus (*Labiosimplex*) *turnbulli* Smales & Chilton, 1997, pp. 197, 199–200.
Labiosimplex turnbulli: Smales, 2006, p. 99.
Type data: holotype SAM AHC 30031, allotype SAM AHC 30100, paratypes SAM AHC 4970.
Type locality: Tenterfield, NSW (29° 04′S 152° 01′S).
Type host: *Notamacropus parryi* (Bennett, 1835).
Site in host: stomach.
Distribution: north-eastern NSW.
Diagnostic features (Fig. 25 M): Males 21–24 mm; females 31–35 mm; oesophago-intestinal diverticula prominent; external branchlets of dorsal ray arise just anterior to principal bifurcation; spicules 5.61–7.75 mm; spicule tips curved, asymmetrical, left spicule more curved than right; ala extending almost to spicule tip; female tail conical, 0.90–1.01 mm; vagina straight, 1.20–1.40 mm long; ovejector J-shaped.

Labiostrongylus Yorke & Maplestone, 1926

Type species: *L. labiostrongylus* Yorke & Maplestone, 1926
Other species: *L. arnhemensis* Smales, 2006; *L. biakensis* Purwaningsih, 2010; *L. grandis* Johnston & Mawson, 1938; *L. macropodis* Johnston & Mawson, 1938 sp. inq.; *L. nabarlekensis* Smales, 1994.

Generic definition: cephalic collar absent; cervical cuticle not inflated; 6 large lips with pulp cavity present; sub-median papillae and amphids borne on lips with 2 interlabia in dorsal and ventral positions; buccal capsule shallow, wider than long, without transverse striations; oesophagus claviform without distinct corpus, isthmus and bulb; nerve ring, deirid and excretory pore in anterior oesophageal region; oesophago-intestinal diverticula present; gubernaculum present; ovejector J or Y-shaped.

Key to species of Labiostrongylus

1a. Spicules > 9.5 mm; tip of female tail blunt . . . . . *L. grandis*
1b. Spicules < 6.0 mm; tip of female pointed 2

2a. Spicules < 4.0 mm; female tail without mucro . . . . . *L. nabarlekensis*
2b. Spicules > 4.0 mm; female tail with or without mucro 3

3a. Spicules straight . . . . . *L. labiostrongylus*
3b. Distal region of spicule deviated dorsally (Fig. 26 G,I) 4

4a. Oesophago-intestinal diverticula bilobed, outer margin convex (Fig. 26 F); tail of female with mucro . . . . . *L. arnhemensis*
4b. Oesophago-intestinal diverticula 4-lobed, outer margin concave (Fig. 26 H); tail of female without mucro . . . . . *L. biakensis*

Labiostrongylus arnhemensis Smales, 2006

Labiostrongylus arnhemensis Smales, 2006, pp. 94–98, figs 52–70.
Labiostrongylus (Labiosimplex) sp.: Smales, 1995, p. 238.
Type data: holotype SAM AHC 32896, allotype SAM AHC 32897, paratypes SAM AHC 6386.
Type locality: Jabiluka, NT (12° 32′S 132° 55′E).
Type host: *Osphranter bernardus* (Rothschild, 1904).
Other hosts: *Notamacropus agilis* (Gould, 1842).
Site in host: stomach.
Distribution: NT (Arnhem Land).
Diagnostic features (Fig. 26 G): Males 44–58 mm; females 55–75 mm; oesophago-intestinal diverticula bilobed; dorsal lobe of bursa no longer than lateral lobes; anterior region of dorsal ray longer than region after first division; spicules 4.08–4.76 mm; distal region of spicules deviated dorsally; ala diminishes gradually anterior to tip; female tail pointed with mucro; vagina sinuous; ovejector Y-shaped.
Comments: *Osphranter bernardus* appears to be the primary host of this species. The single report of the species in *N. agilis* is from the type locality where the two macropodid species occur in sympatry (Smales, 2006). It has not been reported from *N. agilis* outside this area (Speare et al., 1983; Beveridge et al., 1998).

Labiostrongylus biakensis Purwaningsih, 2010

Labiostrongylus biakensis Purwaningsih, 2010, pp. 17–20, figs 1–15.
Type data: holotype and allotype MZB Na 236, paratypes MZB Na 234, 236.
Type locality: Biak, Schouten Archipelago, Western New Guinea (1° 09′S 136° 02′E).
Type host: *Notamacropus agilis* (Gould, 1842).
Site in host: stomach.
Distribution: Western New Guinea .
Diagnostic features (Figs 26 H, I): Males 22.5–29.7 mm; females 34.1–39.7 mm; oesophago-intestinal diverticula 4-lobed; dorsal lobe of bursa longer than lateral lobes; anterior region of dorsal ray shorter than region after first division; spicules 4.84–5.22 mm; distal region of spicules deviated dorsally; ala diminishes gradually to tip; female tail pointed without mucro; vagina sinuous; ovejector J-shaped.

Labiostrongylus grandis Johnston & Mawson, 1938

Labiostrongylus grandis Johnston & Mawson, 1938, pp. 269–270, figs 18–20; Kung, 1948, pp. 104, 106; Skrjabin et al., 1952, p. 178; Popova, 1960, pp. 98–99, fig. 64; Yamaguti, 1961, p. 406; Smales, 1994, pp. 185–188, figs 1–15; Beveridge et al. 1998, p. 481; Smales, 2006, p. 99; Beveridge, 2020c, p.4.
Zoniolaimus grandis: Johnston & Mawson, 1939a, p. 123.
Type data: holotype SAM V4170, allotype SAM V4171, paratypes SAM AHC 1844–5.
Type locality: Mount Liebig, NT (23° 19′S 131° 22′E).
Type host: *Osphranter robustus* (Gould, 1840).
Site in host: stomach.
Distribution: NT, Qld.
Representative DNA sequence data: ITS1, 2: FR854199.
Diagnostic features (Fig. 26 E): Males 29–43 mm; females

40–50 mm; oesophago-intestinal diverticula 4-lobed; dorsal lobe of bursa no longer than lateral lobes; anterior region of dorsal ray longer than region after first division, internal and external branchlets arise at almost same level; spicules 9.95–10.50 mm; distal region of spicules straight; ala terminates anterior to tip; female tail blunt; vagina sinuous; ovejector J-shaped.

***Labiostrongylus labiostrongylus* Yorke & Maplestone, 1926**

Labiostrongylus labiostrongylus Yorke & Maplestone, 1926, p. 67, fig. 35; Baylis, 1934, p. 129; Kung, 1948, pp. 104–106; Skrjabin et al., 1952, p. 178, fig. 88; Yamaguti, 1961, p. 406; Popova, 1960, pp. 93–94, fig. 60; Speare et al., 1983, pp. 90, 94; Beveridge et al. 1998, p. 481; Smales, 2006, pp. 98–100.

Zoniolaimus labiostrongylus: Johnston & Mawson, 1939a, p. 123.

Zoniolaimus insularis Johnston & Mawson, 1939a, pp. 126–127, figs 8–9.

Labiostrongylus insularis: Kung, 1948, pp. 104, 106; Popova, 1960, p. 100.

Type data: "cotypes" BMNH 1927.7.21.7; syntypes BMNH 1999.11. 16.156–160, 2000.4.10.95–98.

Type locality: Townsville, Qld (19° 15′S 146° 49′S).

Type host: *Notamacropus agilis* (Gould, 1842) (as *Macropus* sp.).

Other hosts: *Petrogale wilkinsi* Thomas, 1926 (as *P. brachyotis* (Gould, 1841)); *Thylogale calabyi* Flannery, 1992 (as *T. brunii* (Schreber, 1778)); *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: NT, Qld, WA (Kimberley Division), PNG.

Representative DNA sequence data: ITS1, 2: FR854198; ITS2: Y10797; 5.8S: Z70732.

Diagnostic features (Figs 26 A–D): Males 38–47 mm; females 58–68 mm; oesophago-intestinal diverticula 4-lobed; dorsal lobe of bursa longer than lateral lobes; anterior region of dorsal ray longer than region after first division, external branchlets arise anterior to major bifurcation; spicules 4.30–5.00 mm; distal region of spicules straight; ala terminates anterior to tip; female tail pointed, with mucro; vagina sinuous; ovejector J-shaped.

Comments: Yorke & Maplestone (1926) provided very few collection details, but as with the other new genera erected in their book, the specimens were from *N. agilis* from Townsville, Qld (Beveridge, 1982). A number of the host identifications given in Smales (1994, 2006) have changed. Current identifications of host names follow Spratt & Beveridge (2016).

***Labiostrongylus macropodis* Johnston & Mawson, 1938 sp. inq.**

Labiostrongylus macropodis Johnston & Mawson, 1938, pp. 266–267, figs 9–14; Kung, 1948, pp. 104, 106; Popova, 1960, pp. 101–103, fig.66; Smales, 1994, pp. 191, 193; 2006, p. 99.

Zoniolaimus macropodis: Johnston & Mawson, 1939a, p. 123.

Type data: holotype female, SAM V2765.

Type locality: Mount Liebig, NT (23° 19′S 131° 22′E).

Type host: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

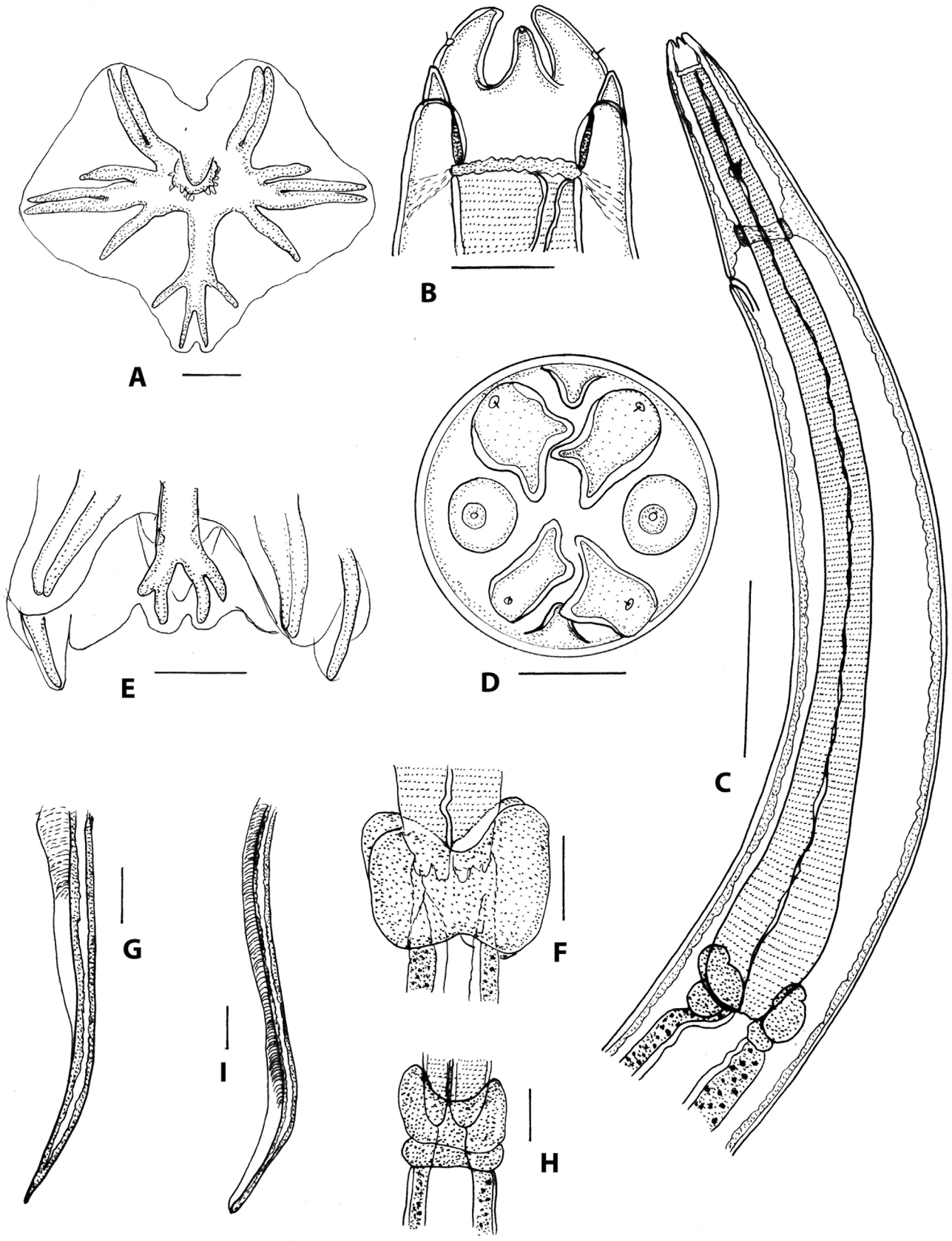
Distribution: NT.

Diagnostic features (from Johnston & Mawson, 1938): Males 21–30 mm; females 24.8–31.2 mm; oesophago-intestinal diverticula present; dorsal lobe of bursa no longer than lateral lobes; anterior region of dorsal ray short, external branchlets arise at same level as internals, all very short; spicules 9.4–11.1 mm; female tail blunt; vagina sinuous; ovejector J-shaped.

Comments: Smales (1994) reviewed this species but with only a single female available was unable to draw any firm conclusions as to its identity. She noted that it was very similar to *L. grandis* and that both occurred in the same host at the type locality. In addition, the spicule measurements given by Johnston & Mawson (1938) align the species with *L. grandis*. The differences in the dorsal ray between *L. grandis* and *L. macropodis* are probably due to within species variation (Smales, 1994). If the two species are synonyms, then *L. macropodis* has page priority. Smales (1994) treated this species as *inquirenda*.

Fig. 26. Genus *Labiostrongylus*. A, *Labiostrongylus labiostrongylus*, bursa, apical view; B, *L. labiostrongylus*, buccal capsule, dorso-ventral view; C, *L. labiostrongylus*, anterior end, lateral view; D, *L. labiostrongylus*, mouth opening, apical view; E, *Labiostrongylus grandis*, dorsal lobe of bursa, dorsal view; F, *Labiostrongylus arnhemensis*, oesophago-intestinal junction; G, *Labiostrongylus arnhemensis*, spicule tip; H, *Labiostrongylus biakensis*, oesophago-intestinal junction; I, *L. biakensis,* spicule tip. (A, E, from Smales, 1994; B–D, original; F, G, from Smales, 2006).

Scale-bars: A, E, H, 0.2 mm; B, D, 0.1 mm; C, 1.0 mm; F. 0.4 mm; G, 0.025 mm; 1, 0.5 mm.


A
B
C
D
E
F
G
H
I

***Labiostrongylus nabarlekensis* Smales, 1994**

Labiostrongylus nabarlekensis Smales, 1994, pp. 189–191, figs. 30–46.

Type data: holotype SAM V4160, allotype SAM V4161, paratypes SAM AHC 10833.

Type locality: Nabarlek, NT (12° 18′S 133° 19′E).

Type host: *Petrogale wilkinsi* Thomas, 1926 (as *P. brachyotis* (Gould, 1841)).

Other hosts: *Petrogale brachyotis* (Gould, 1841).

Site in host: stomach.

Distribution: NT, WA (Kimberley Division).

Diagnostic features: Males 25–32 mm; females 37–42 mm; oesophago-intestinal diverticula 4-lobed; dorsal lobe of bursa no longer than lateral lobes; anterior region of dorsal ray longer than region after first division, external branchlets arise anterior to internals; spicules 3.45–3.90 mm; distal region of spicules straight; ala terminates anterior to tip; female tail pointed, without mucro; vagina sinuous; ovejector Y-shaped.

Macroponema Mawson, 1978

Type species: *M. comani* Mawson, 1978.

Other species: *M. arundeli* Beveridge, 2020, *M. beveridgei* Mawson, 1978, *M. obendorfi* Beveridge, 2020.

Generic diagnosis: cephalic collar absent; submedial papillae conical with paired setae; mouth opening and buccal capsule dorsoventrally elongate; buccal capsule wider than long, walls poorly sclerotized, supported externally by strong radial musculature; poorly defined annulus surrounds buccal capsule; oesophageal corpus elongate, lined with sclerotised thickenings; isthmus indistinct; bulb elongate; nerve ring in anterior oesophageal region; derids at level of buccal capsule; excretory pore at level of oesophago-intestinal junction; bursa without sclerotized bosses; gubernaculum absent; spicules elongate, alate; vulva anterior to anus; ovejector J-shaped.

Comments: Species of this genus, although characterised primarily by the features of the buccal capsule, are most readily identifiable based on the ornamentation of the oesophagus. For this reason, most of the illustrations provided relate to these readily identifiable characters.

Key to species of Macroponema

1a. Oesophageal corpus with bead-like sclerotisations lining lumen (Fig. 27 J) 2

1b. Oesophageal corpus without bead-like sclerotisations lining lumen (Figs 27 H, I) 3

2a. With c. 20 sets of bead–like sclerotisations . . . . . *M. comani*

2b. With c. 14 sets of bead–like sclerotisations . . . . . *M. obendorfi*

3a. Oesophageal corpus with transverse sclerotisations along lumen (Fig. 27 I) . . . . . *M. beveridgei*

3b. Oesophageal corpus with longitudinal a rcuate sclerotisations along lumen (Fig. 27 H) . . . . . *M. arundeli*

***Macroponema arundeli* Beveridge, 2020**

Macroponema arundeli Beveridge, 2020 in Sukee et al., 2020, pp. 4–5, figs 1–13.

Type data: holotype SAM AHC 48933, allotype SAM AHC 48934, paratypes SAM AHC 48935.

Type locality: 53 km north of The Lynd Junction, Qld (18° 53′S, 144° 33′E).

Type host: *Macropus giganteus* Shaw, 1790.

Site in host: stomach.

Distribution: Qld, northern NSW. Map: Sukee et al., 2020, p. 8.

Representative DNA sequence data: ITS1, 2: MT 080011.

Diagnostic features (Figs 27 A, E, F, H): Males 19–25 mm long; females 37–70 mm long; buccal capsule with annulus in anterior region; oesophageal corpus with longitudinal arcuate sclerotisations, arranged in groups of 3, one from each sector of the oesophagus; spicules 1.95–2.14 mm; spicule ala terminates abruptly anterior to spicule tip; genital cone with paired bifid appendages; female tail directed slightly dorsally; ovejector J-shaped.

***Macroponema beveridgei* Mawson, 1978**

Macroponema beveridgei Mawson, 1978, pp. 163–165, figs 1–8; Beveridge et al., 1998, p. 483; Beveridge, 2020c, p. 5.

Type data: holotype SAM AHC 41154, allotype SAM AHC 41155.

Type locality: Elizabeth Downs Station via Adelaide River, NT (13° 38′S, 130° 29′E).

Type host: *Osphranter antilopinus* (Gould, 1842).

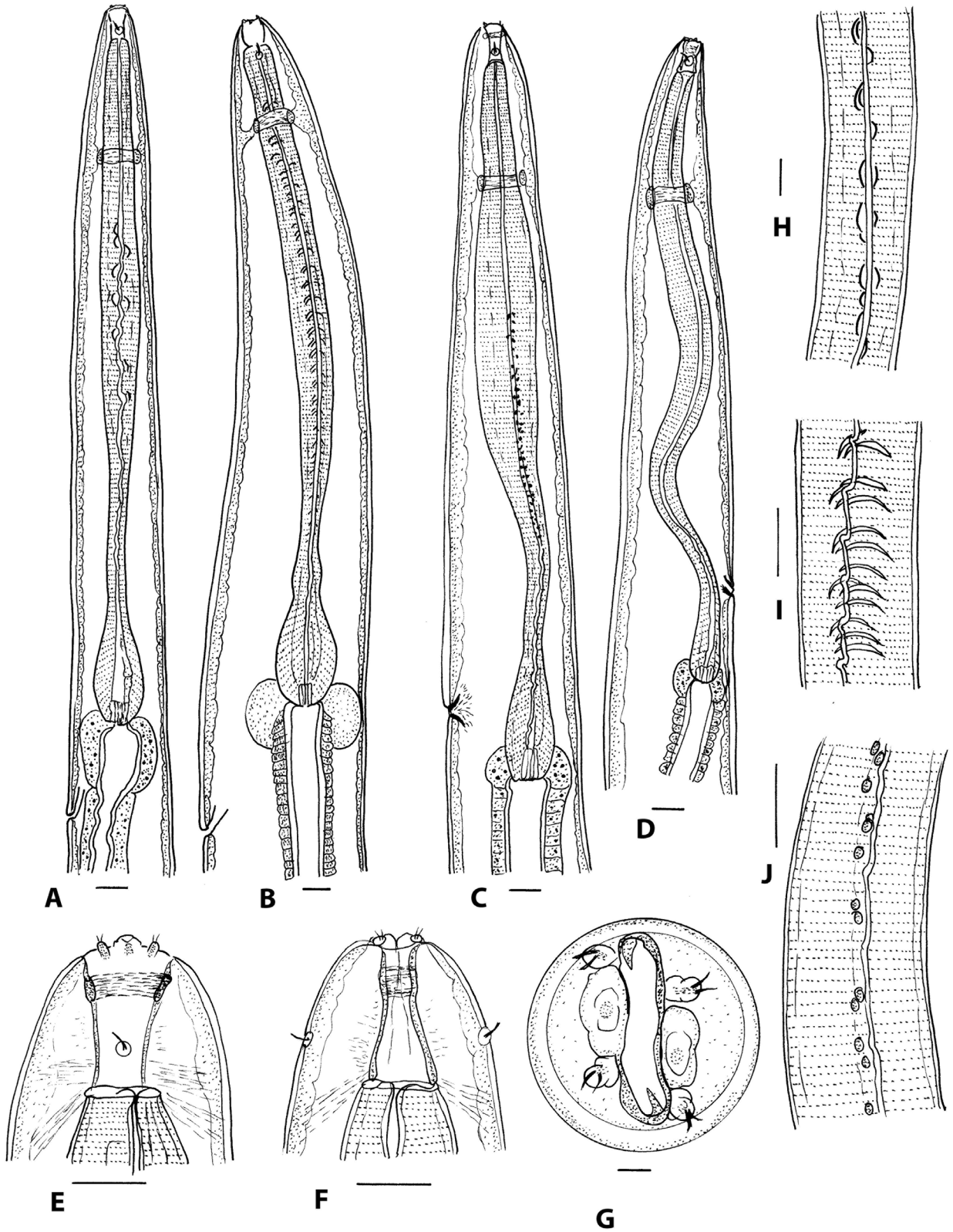


Fig. 27. Genus *Macroponema*. A, *Macroponema arundeli*, oesophagus, lateral view; B, *M. beveridgei*, oesophagus, lateral view; C, *M. comani*, oesophagus, lateral view; D, *M. obendorfi*, oesophagus, lateral view; E, F, *M. arundeli*, buccal capsule, lateral and dorso-ventral views; G, *M. obendorfi*, anterior end, apical view; H–J, detail of oesophageal ornamentation in *M. arundeli* (H), *M. beveridgei* (I) and *M. comani* (J). (A–J from Sukee et al., 2020).

Scale-bars: 0.1 mm.

Other hosts: *Osphranter robustus* (Gould, 1840).
Site in host: stomach.
Distribution: NT (Top End), WA (Kimberley Division), Qld, north-eastern NSW. Map: Sukee et al., 2020, p. 13.
Representative DNA sequence data: ITS1, 2: MT 080016.
Diagnostic features (Figs 27 B, I): Males 15–20 mm; females 40–62 mm; buccal capsule with annulus at posterior end; oesophageal corpus with transverse sclerotisations, arranged in groups of 3, one from each sector of the oesophagus; spicules 1.77–2.12 mm; spicule ala diminishes gradually in width towards spicule tip; genital cone with paired bifid appendages and numerous smaller appendages arranged in 2 arcs; female tail directed posteriorly; ovejector J-shaped.
Comments: Mawson (1978) and Spratt & Beveridge (2016) included *N. agilis* and *Wal. bicolor* as hosts, but the record from *N. agilis* is an error for *Macropostrongylus* and no specimens are available to confirm the record from *Wal. bicolor* (Sukee et al., 2020). Chilton et al. (2018) listed *Notamacropus dorsalis* as a host and provided confirmatory sequence data (MG957433; SAM AHC 48213) but this may be a host misidentification as the nematode species has not been collected from additional specimens of this host (Beveridge et al., 1998).

***Macroponema comani* Mawson, 1978**

Macroponema comani Mawson, 1978, pp. 165–166, figs 9–19; Beveridge & Arundel, 1979, p. 72; Beveridge, 1986e, p. 779–781, fig 2 A–F; Arundel et al., 1990, p. 42; Beveridge et al., 1998, p. 483; Spratt et al., 2017, p. 240; Sukee et al., 2020, pp. 12–14, figs 29–44.
Type data: holotype SAM AHC 41156, allotype SAM AHC 41157.
Type locality: Yan Yean, Vic. (37° 34'S 145° 06'E).
Type host: *Macropus giganteus* Shaw, 1790.
Site in host: stomach.
Distribution: Qld, NSW, ACT, Vic. Map: Sukee et al., 2020, p. 17.
Representative DNA sequence data: ITS1, 2: MT 080023.
Diagnostic features (Figs 27 C, J): Males 10–17 mm; females 18–27 mm; buccal capsule with annulus in anterior region; oesophageal corpus with c. 20 sets of bead-like sclerotisations, arranged in groups of 3, one from each sector of the oesophagus; spicules 1.70–1.98 mm; spicule ala diminishes gradually in width towards spicule tip; genital cone with paired bifid appendages; female tail directed posteriorly; ovejector J-shaped.

***Macroponema obendorfi* Beveridge , 2020**

Macroponema obendorfi Beveridge, 2020 in Sukee et al., 2020, pp. 14, 17–20, figs 46–55.
Macroponema cf *comani* of Tan et al., 2012, pp. 170–172.
Type data: holotype SAM AHC 48936, allotype SAM AHC 48937, paratypes SAM AHC 48938.
Type locality: Mount Smith, NT (13° 31'S, 131° 7'E).
Type host: *Osphranter robustus* (Gould, 1840).
Other hosts: *Osphranter antilopinus* (Gould, 1842).
Site in host: stomach.
Distribution: NT (Top End); WA (KimberleyDivision). Map: Sukee et al., 2020, p. 20.
Representative DNA sequence data: ITS1, 2: HE 775532.
Diagnostic features (Figs 27 D, G): Males 8.3–11.1 mm; females 11.3–13.8 mm; buccal capsule with annulus in anterior region; oesophageal corpus with c. 14 sets of bead-like sclerotisations, arranged in groups of 3, one from each sector of the oesophagus; spicules 1.43–1.80 mm; spicule ala diminishes gradually in width towards spicule tip; genital cone with paired bifid appendages; female tail directed posteriorly; ovejector J-shaped.
Comments: This species was first recognised as a cryptic species within *M. comani* by Tan et al. (2010). The species differ only in the pattern of oesophageal ornamentation and spicule lengths but occur allopatrically in different host species.

Macropostrongylus Yorke & Maplestone, 1926

Syn. *Gelanostrongylus* Popova, 1952 in Skrjabin et al., 1952, p. 785.
Type species: *Ma. macropostrongylus* Yorke & Maplestone, 1926.
Other species: *Ma. lesouefi* Johnston & Mawson, 1939; *Ma. macrostoma* Davey & Wood, 1938; *Ma. petrogale* Beveridge, 1986; *Ma. spearei* Beveridge, 1986; *Ma. yorkei* Baylis, 1927.
Nomen nudum: *Ma. irma* Johnston & Mawson, 1940 (see Mawson, 1977b).

Generic diagnosis: cephalic collar present; mouth opening sub-triangular to dorso-ventrally elongate; cephalic papillae conical with single or paired setae; amphids prominent; buccal capsule slightly longer than wide, poorly sclerotized, without transverse striations; some species with annulus in posterior half; walls of buccal capsule supported externally

by prominent radial musculature; anterior extremity of buccal capsule with 0, 2, 4 or 8 lip-like protrusions into lumen of capsule; oesophageal corpus elongate, isthmus indistinct, bulb fusiform; nerve ring in anterior oesophageal region; deirid posterior to buccal capsule; excretory pore at or posterior to oesophago-intestinal junction or in mid-oesophageal region; anterior extremity of intestine often expanded but not enclosing bulb; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum absent; vulva immediately anterior to anus; ovejector J- or Y-shaped.

Comments: The species of this genus are most readily identified by the features of the amphids, oesophagus and, in one case, the deirid. None of the material of *Ma. lesouefi* available was suitable for illustration.

Key to species of Macropostrongylus

1a. Amphids borne on prominent conical projections (Fig. 28 G); excretory pore in anterior oesophageal region (Fig. 28 A); no annulus in posterior region of buccal capsule (Fig. 28 G) 2

1b. Amphids borne on low, dome-shaped projections (Figs 28 H, I); excretory pore in region of oesophago-intestinal junction (Fig. 28 B); annulus in posterior region of buccal capsule (Figs 28 H, I) 3

2a. Spicules 1.65–1.70 mm . . . *Ma. macropostrongylus*

2b. Spicules 0.36–0.70 mm. . . . . *Ma. lesouefi*

3a. Spicules 0.41–0.56 mm; deirid bifid (Fig. 28 C) . . . . . *Ma. petrogale*

3b. Spicules > 0.68 mm; deirid simple 4

4a. Oesophageal bulb c. 30% of total oesophageal length; corpus of uniform diameter (Fig. 28 B); spicules 1.64–2.63 mm long; vagina J–shaped . . . . . *Ma. spearei*

4b. Oesophageal bulb < 25% of total oesophageal length; anterior region of corpus much wider than posterior region (Figs 28 E, F); spicules < 1.12 mm long; vagina Y-shaped 5

5a. Spicules 0.68–0.76 mm long; buccal capsule wider than long (Fig. 28 H) . . . . . *Ma. yorkei*

5b. Spicules 1.02–1.12 mm long; buccal capsule longer than wide (Fig. 28 I) . . *Ma. macrostoma*

***Macropostrongylus lesouefi* Johnston & Mawson, 1939**

Macropostrongylus lesouefi Johnston & Mawson, 1939b, p. 525, figs 31–32; Mawson, 1977b, pp. 54–56, figs 20–24; Skrjabin et al., 1952, p. 292.

Gelanostrongylus lesouefi: Popova, 1952, p. 786, 1960, pp. 88–89, fig. 57; Yamaguti, 1961, p. 405.

Type data: holotype SAM AHC 42830, allotype SAM AHC 42831, paratypes SAM AHC 2678.

Type locality: Sydney Zoological Gardens, NSW (33° 53′S 151° 13′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817) (as *Macropus ruficollis* (Desmarest, 1817).

Site in host: stomach.

Distribution: NSW (captive).

Diagnostic features: Male 6.2–8.4 mm; female 10.7 mm; amphids on conical projections; nerve ring in anterior oesophageal region; deirids in post-buccal region; spicules 0.36–0.70 mm.

Comment: This species has not been encountered since its original description in a zoo animal, despite several surveys of the parasites of wild *N. rufogriseus* (Aussavy et al., 2011; Spratt et al., 2017). The only available descriptions of the species are brief (Johnston & Mawson, 1939b; Mawson 1977b) and more data are needed before any judgement can be made on its status. The type material was re-examined but is in a poor state of preservation and no additional details could be added.

***Macropostrongylus macropostrongylus* Yorke & Maplestone, 1926**

Macropostrongylus macropostrongylus Yorke & Maplestone, 1926, p. 75, figs 40 A–E; Baylis, 1934, p. 129; Johnston & Mawson, 1939a, p. 143; 1939c, p. 209, fig. 8; Skrjabin et al., 1952, p. 291; Popova, 1958, p. 252; Yamaguti, 1961, p. 384; Mawson, 1977b, pp. 52–54, figs. 1–7; Speare et al., 1983, p. 90; Beveridge, 1985, pp. 762–765, fig. 1; Beveridge et al., 1989, p. 277; 1998, p. 483; Beveridge, 2020c, p. 5.

Type data: syntypes in BMNH 1927.7.21.2–3.

Type locality: Townsville, Qld (19° 15′S 146° 49′E).

Type host: *Notamacropus agilis* (Gould, 1842) (as *Macropus* sp.).

Other hosts: *Notamacropus dorsalis* (Gray, 1837); *Notamacropus parryi* (Bennett, 1835); *Osphranter robustus* (Gould, 1840); *Petrogale godmani* Thomas, 1923; *Wallabia bicolor* (Desmarest, 1804); *Thylogale brunii* (Schreber, 1778) (possible record in error).

Site in host: stomach.

Distribution: NT, Qld, PNG.

Representative DNA sequence data: ITS1, 2: MG 865626.
Diagnostic features (Figs 28 A, G, J): Males 8.2–10.7 mm; females 9.3–11.2 mm; amphids on prominent conical projections; cephalic papillae with single seta (in Beveridge, 1986a, paired in Johnston & Mawson, 1939c and Mawson, 1977b); buccal capsule without annulus, anterior extremity forming 8 lip–like projections into lumen of capsule; oesophageal corpus of uniform width; excretory pore in mid-oesophageal region; spicules 1.65–1.70 mm; spicule ala terminates abruptly anterior to spicule tip; ovejector J-shaped.
Comment: *Notamacropus agilis* appears to be the primary host of this parasite with occurrences in other sympatric hosts representing incidental infections (Beveridge et al., 1998).

***Macropostrongylus macrostoma* Davey & Wood, 1938**
Macropostrongylus macrostoma Davey & Wood, 1938, p. 261, figs 6–8; Mawson, 1977b, p. 54, figs 8–12, 47; Beveridge, 1985, pp. 772–775, figs 5–6; Beveridge et al., 1998, p. 483.
Macropostrongylus yorkei Baylis, 1927 of Johnston & Mawson, 1939a, p. 143, corrected in Mawson, 1977b, p. 54.
Gelanostrongylus macrostomus: Popova, 1952, p. 785; 1960, pp. 81–82, fig. 51 in Skrjabin et al., 1952, p. 176.
Gelanostrongylus macrostoma: Yamaguti, p. 405.
Type data: syntypes BMNH 1939.1.10.108–130.
Type locality: Townsville, Qld (19° 15′S 146° 49′E).
Type host: *Osphranter robustus* (Gould, 1840) (as *Macropus robustus* Gould, 1840) (a probable error for *Notamacropus parryi* (Bennett, 1835).
Other hosts: *Notamacropus parryi* (Bennett, 1835).
Distribution: Qld.
Representative DNA sequence data: ITS1, 2: MG 865627.
Diagnostic features (Figs 28 F, I, M): Males 9.6–13.2 mm; females 24–39 mm; amphids on low, dome-shaped projections; cephalic papillae with single seta; buccal capsule with annulus, anterior extremity forming 4 lip-like projections into lumen of capsule; anterior region of oesophageal corpus wider than posterior region; excretory pore near oesophago-intestinal junction; spicules 1.02–1.12 mm; spicule ala enlarges at spicule tip; ovejector Y-shaped.
Comment: Apart from its original description, this species has only been found in *N. parryi* (see Beveridge, 1985; Beveridge et al., 1998) suggesting that the original host identification (*O. robustus*) was incorrect. The same apparent error in host identification applies to *Pharyngostrongylus ornatus*.

***Macropostrongylus petrogale* Beveridge, 1985**
Macropostrongylus petrogale Beveridge, 1985, pp. 765–767, fig. 2; Beveridge et al., 1989, p. 277.
Type data: holotype SAM V3562, allotype SAM V3563, paratypes SAM V3564, SAM AHC 13391–13392, MNHNP 530HD.
Type locality: Hillsborough Station via Ravenswood, Qld (20° 1′S 146° 59′E).
Type host: *Petrogale assimilis* Ramsay, 1877.
Other hosts: *Petrogale godmani* Thomas, 1923.
Site in host: stomach.
Distribution: Qld.
Representative DNA sequence data: ITS1, 2: MG 865628.
Diagnostic features (Figs 28 C, D): Males 5.6–7.2 mm; females 9.2–11.1 mm; amphids on low, dome-shaped projections; cephalic papillae with paired setae; buccal capsule with annulus, anterior extremity forming 2 lateral, lip-like projections into lumen of capsule; anterior region of oesophageal corpus wider than posterior region; deirid bifid; excretory pore near oesophago-intestinal junction; spicules 0.41–0.56 mm; spicule ala diminishes gradually towards spicule tip; ovejector Y-shaped.
Comments: This species appears to be confined to rock wallabies (*Petrogale* spp.) in Queensland.

***Macropostrongylus spearei* Beveridge, 1985**
Macropostrongylus spearei Beveridge, 1985, pp. 776–778, fig. 7; Beveridge et al., 1998, p. 483; Beveridge, 2020c, p. 5.
Type data: holotype SAM V3566, allotype SAM V3567, paratypes SAM V3568–3577, SAM AHC 13498–13503, MNHNP 531 HD.
Type locality: Harvest Home Station via Charter Towers, Qld (20° 42′ S 146° 38′E).
Type host: *Osphranter robustus* (Gould, 1840).
Site in host: stomach.
Distribution: Qld.
Representative DNA sequence data: ITS1, 2: OM987392, OM987393 (unpublished; voucher specimens SAM AHC 48930, 48931).
Diagnostic features: Males 9.3–11.1 mm; females 6–18 mm; amphids on low, dome-shaped projections; cephalic papillae with single seta; buccal capsule with annulus, anterior extremity without lip-like projections into lumen of capsule; oesophageal corpus of uniform diameter; excretory pore near oesophago-intestinal junction; spicules 1.64–2.43 mm; spicule ala diminishes gradually towards spicule tip; ovejector J-shaped.
Comments: This species appears to be limited to *O. robustus* in Queensland (Beveridge et al., 1998).

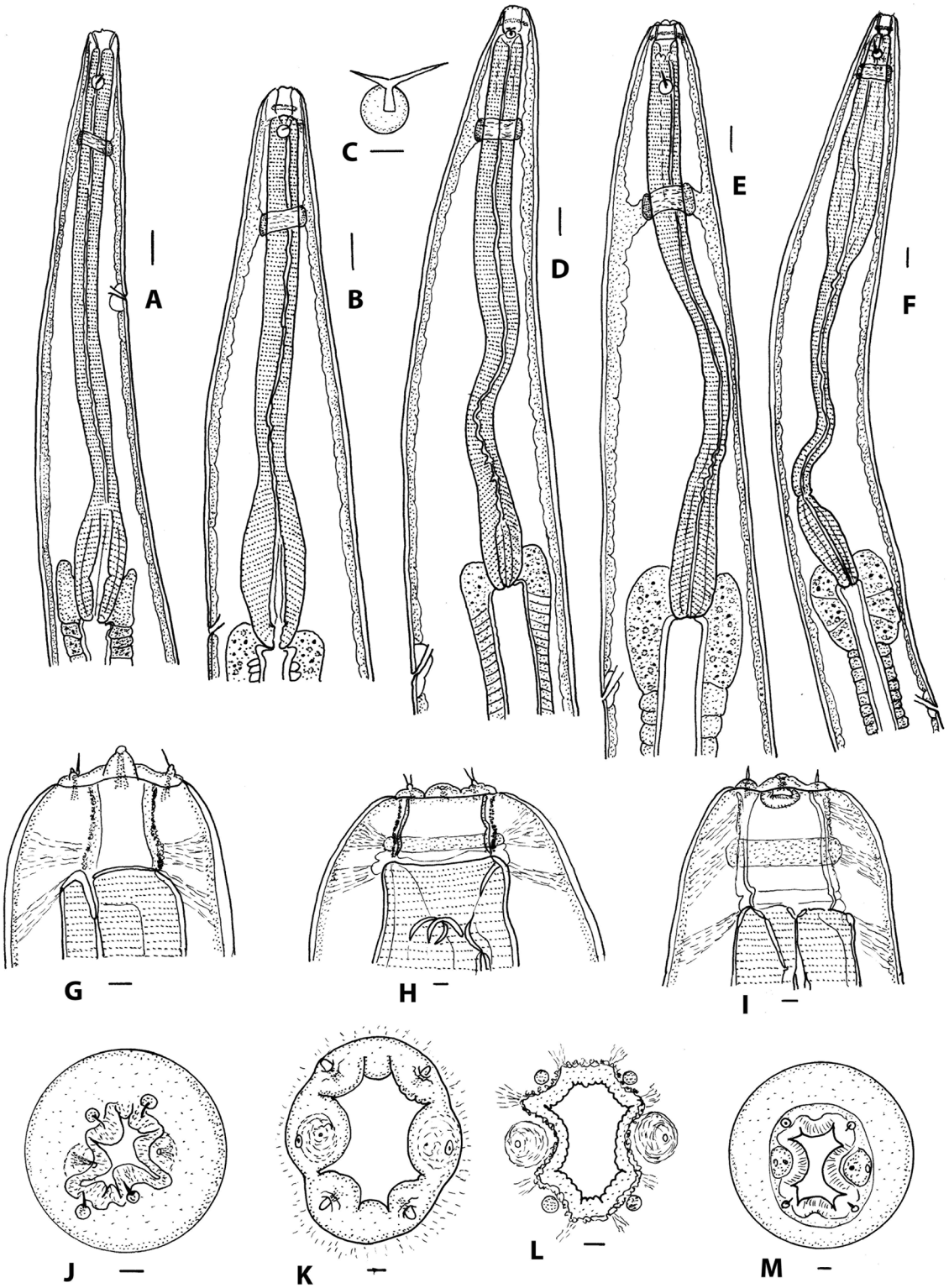


Fig. 28. Genus *Macropostrongylus*. A, *Macropostrongylus macropostrongylus*, oesophagus, lateral view; B, *Ma. spearei*, oesophagus, lateral view; C, *Ma. petrogale*, deirid, lateral view; D, *Ma. petrogale*, oesophagus, lateral view; E, *Ma. yorkei*, oesophagus, lateral view; F, *Ma. macrostoma*, oesophagus, lateral view; G, *Ma. macropostrongylus*, buccal capsule, lateral view; H, *Ma. yorkei*, buccal capsule, lateral view; I, *Ma. macrostoma*, buccal capsule, lateral view; J, *Ma. macropostrongylus*, anterior end, apical view; K, *Ma. yorkei*, anterior end, apical view; L, *Ma. yorkei*, optical transverse section through buccal capsule; M, *Ma. macrostoma*, anterior end, apical view. (A–M from Beveridge, 1985).

Scale-bars: A, B, D–F, 0.1 mm; C, G–M, 0.01 mm.

***Macropostrongylus yorkei* Baylis, 1927**

Macropostrongylus yorkei Baylis, 1927, pp. 215–218, figs 1–3; Baylis, 1934, p.129; Johnston & Mawson, 1939a, p. 143; 1939c, p. 209, figs 6–7; Skrjabin et al., 1952, p. 191; Mawson, 1977b, p. 54, figs 13–19, 51; Speare et al., 1983, p. 90; Beveridge, 1985, pp. 768–771, figs 3, 4; Beveridge et al., 1989, p. 277.

Gelanostrongylus yorkei: Popova, 1952, p. 786, in Skrjabin et al., 1952; 1960, pp. 90–91, fig 59; Yamaguti, 1961, p. 405.

Type data: syntypes BMNH 1927.8.10.57–71.

Type locality: Townsville, Qld (19° 15′S 146° 49′E).

Type host: *Notamacropus agilis* (Gould, 1842).

Site in host: stomach.

Distribution: NT, Qld, PNG.

Representative DNA sequence data: ITS1, 2: MG 865629.

Diagnostic features (Figs 28 E, H, K, L): Males 10–12 mm; females 18–23 mm; amphids on low, dome-shaped projections; cephalic papillae with paired setae; buccal capsule with annulus; anterior region without lip-like projections into lumen of capsule; anterior region of oesophageal corpus wider than posterior region; excretory pore near oesophago-intestinal junction; spicules 0.68–0.76 mm; spicule ala enlarges at spicule tip; ovejector Y-shaped.

Mbaisonema Beveridge, 1997

Type species: *Mb. coronatum* Beveridge, 1997.

Generic diagnosis: Cephalic collar present; cephalic papillae conical with paired elongate setae; mouth opening circular; labial crown of numerous elements present; buccal capsule wider than long, diminishing in width posteriorly; anterior buccal capsule with highly refractile annulus, posterior part thin-walled; 4 lip-like expansions of buccal capsule and labial collar projecting into lumen; oesophageal corpus cylindrical, bulb ovoid without sclerotized plates; nerve ring in middle of oesophageal corpus; excretory pore near posterior end of oesophageal corpus; deirid in anterior oesophageal region; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum replaced by thickening of dorsal wall of cloaca; ovejector Y-shaped.

Comments: This monotypic genus is readily recognisable with a labial crown of numerous elements and the anterior sclerotisation of the buccal capsule. It is known only from an endangered species of tree kangaroo occurring above the tree line in the mountains of Western New Guinea (Flannery, 1995).

***Mbaisonema coronatum* Beveridge, 1997**

Mbaisonema coronatum Beveridge, 1997, pp. 28–30, figs 17–30.

Type data: holotype SAM AHC 30408, allotype SAM AHC 30409, paratypes SAM AHC 30410.

Type locality: Gunung Ki, Tembagapura, Western New Guinea (4° 05′S 137° 06′E).

Type host: *Dendrolagus mbaiso* Flannery, Boeadi & Szaley, 1995.

Site in host: stomach.

Distribution: Western New Guinea.

Diagnostic features (Figs 29 A–D): Males 3.9–4.5 mm; females 4.4–5.2 mm; dorsal lobe of bursa elongate; internal branchlets of dorsal ray long, slender; external branchlets vestigial; spicules 0.42–0.46 mm; ovejector Y-shaped.

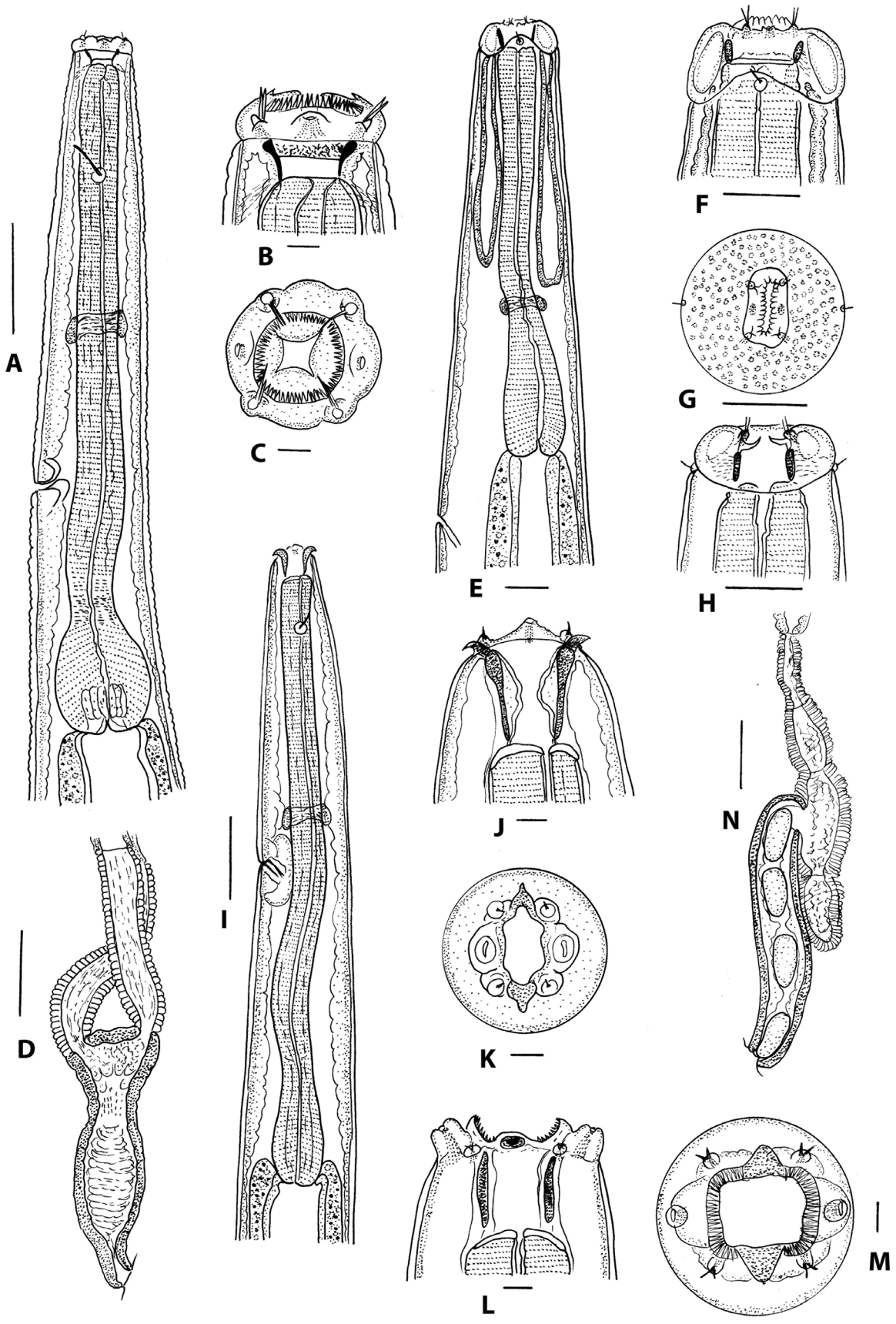
Monilonema Beveridge & Johnson, 1981

Type species: *Mo. lacunosum* Beveridge & Johnson, 1981.

Generic definition: large cervical collar present with subcuticular cavity surrounding anterior end, arcing anteriorly around deirid on lateral surfaces; cephalic collar present; cephalic papillae conical with paired setae; mouth opening and buccal capsule dorsoventrally elongate; labial crown of approximately 20 elements; buccal capsule wider than long in lateral view, poorly sclerotized, without transverse striations, supported externally by prominent radial

Fig. 29. Genera *Mbasionema*, *Monilonema* and *Papillostrongylus*. A, *Mbaisonema coronatum*, oesophagus, lateral view; B, *Mb. coronatum*, buccal capsule, lateral view; C, *Mb. coronatum*, anterior end, apical view; D, *Mb. coronatum*, ovejector, lateral view; E, *Monilonema lacunosum*, oesophagus, lateral view; F, *Mo. lacunosum,* buccal capsule, lateral view; G, *Mo. lacunosum*, anterior end, apical view; H, *Mo. lacunosum*, optical section through buccal capsule; I, *Papillostrongylus labiatus*, oesophagus, lateral view; J, *P. labiatus*, buccal capsule, lateral view; K, *P. labiatus*, anterior end, apical view; L, *Papillostrongylus barbatus*, buccal capsule, lateral view; M, *P. barbatus*, anterior end, apical view; N, *P. labiatus*, ovejector**.** (A–D from Beveridge, 1997, E–H from Beveridge & Johnson, 1981; I–N from Chilton et al., 2002).

Scale-bars: A, D, E–I, N, 0.1 mm; B, C, J–M. 0.01 mm.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muscles; paired dorsal and ventral tubular structures extend from buccal capsule to level of nerve ring; nerve ring surrounds oesophageal isthmus; deirid post buccal; excretory pore near oesophago-intestinal junction; bursa with sclerotized bosses; spicules elongate, alate; gubernaculum present; ovejector J-shaped.

Comments: This genus was originally erected for a single species with four blind, tubular structures extending from the buccal capsule to the nerve ring, *Mo. lacunosum*. Subsequently, a second species, *Mo. ochetocephalum*, was added which also had similar tubules, considered at that time to represent a synapomorphy (Beveridge, 1986a, d). Subsequent molecular studies suggested that this character was homoplasious (Chilton et al., 2018) and that *Mo. ochetocephalum*, represented a separate genus, here identified as a new genus, *Sacculostrongylus* (see below). Beveridge & Johnson (1981) referred to "...a leaf crown-like flange...." at the mouth opening. However, re-examination of their fig. 17 and the scanning electron micrograph (fig. 37) indicate that it is a labial crown.

***Monilonema lacunosum* Beveridge & Johnson, 1981**

Monilonema lacunosum Beveridge & Johnson, 1981, pp. 81–82, figs 14–27, 37 (as *lacunosa*); Beveridge et al., 1992, p. 365; Griffith et al., 2000, p. 310.

Type data: holotype SAM V2007, allotype SAM V2007, paratypes SAM V2008–2026, BMNH 1980.85–86, USNPC 75750.

Type locality: Mission Beach, Qld (17° 52′S 146° 06′E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, 2: MG865630.

Diagnostic features (Figs 29 E–H): Males 6.1–7.6 mm; females 7.2–8.6 mm; spicules 2.00–2.15 mm; ovejector J-shaped.

Papillostrongylus Johnston & Mawson, 1939

Type species: *P. labiatus* Johnston & Mawson, 1939.

Other species: *P. barbatus* Chilton, Huby-Chilton, Gasser & Beveridge, 2002.

Generic diagnosis: Cephalic collar present; cephalic papillae dome-shaped with single or bifid seta(e); amphids on conical elevations; large triangular dorsal and ventral projections between cephalic papillae; leaf crowns present or absent; mouth opening dorsoventrally elongate or quadrangular; buccal capsule highly sclerotized, urceolate, wider anteriorly, continuous with dorsal and ventral projections; inner lining of buccal capsule membranous; oesophagus short, corpus cylindrical, bulb ovoid, without sclerotized plates; nerve ring in mid-oesophageal region; excretory pore immediately posterior to nerve ring; deirid in anterior oesophageal region; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum absent; ovejector J-shaped.

Comments: Molecular data suggest that the genus may be paraphyletic (Chilton et al., 2018).

Key to species of Papillostrongylus

1a. Prominent external leaf crown on lateral sides of mouth opening (Figs 29 L, M) *P. barbatus*

1b. Mouth opening without leaf crown elements (Figs 29 J, K) . . . . . *P. labiatus*

***Papillostrongylus barbatus* Chilton, Huby-Chilton, Gasser & Beveridge, 2002**

Papillostrongylus barbatus Chilton, Huby-Chilton, Gasser & Beveridge, 2002, pp. 85–89, figs 13–24, 26–27; Beveridge, 2020c, p. 6.

Papillostrongylus papillatus: Mawson, 1964, pp. 243–244, figs 26–31; Mykytowycz, 1964, p. 682; Arundel et al., 1979, pp. 365, 370; Beveridge & Arundel, 1979, p. 72; Beveridge et al., 1989, p. 277, 1998, p. 483.

Type data: holotype SAM AHC 31384, allotype SAM AHC 31385, paratypes SAM AHC 11644, BMNH 2000.8.3.12–15, USNPC 90610.

Type locality: Oban Station via Mount Isa, Qld (21° 14′S 139° 3′E).

Type host: *Osphranter rufus* (Desmarest, 1822).

Other hosts: *Osphranter robustus* (Gould, 1840); *Macropus fuliginosus* (Desmarest, 1817); *Macropus giganteus* Shaw, 1790; *Petrogale assimilis* Ramsay, 1877; *Petrogale purpureicollis* Le Souef, 1924.

Site in host: stomach.

Distribution: Qld, western NSW, northern SA, north-western WA. Map: Chilton et al., 2002, p. 88.

Representative DNA sequence data: ITS1, 2: AJ309961.

Diagnostic features (Figs 29 L, M, 30 B–D): Males 8.5–12.0 mm; 11.7–15.3 mm; cephalic papillae with paired setae; mouth opening quadrangular; leaf crown of numerous elements along lateral margins of mouth opening; spicules 2.35–2.78 mm; ovejector J-shaped.

Comments: This species was initially included within *P. labiatus*.

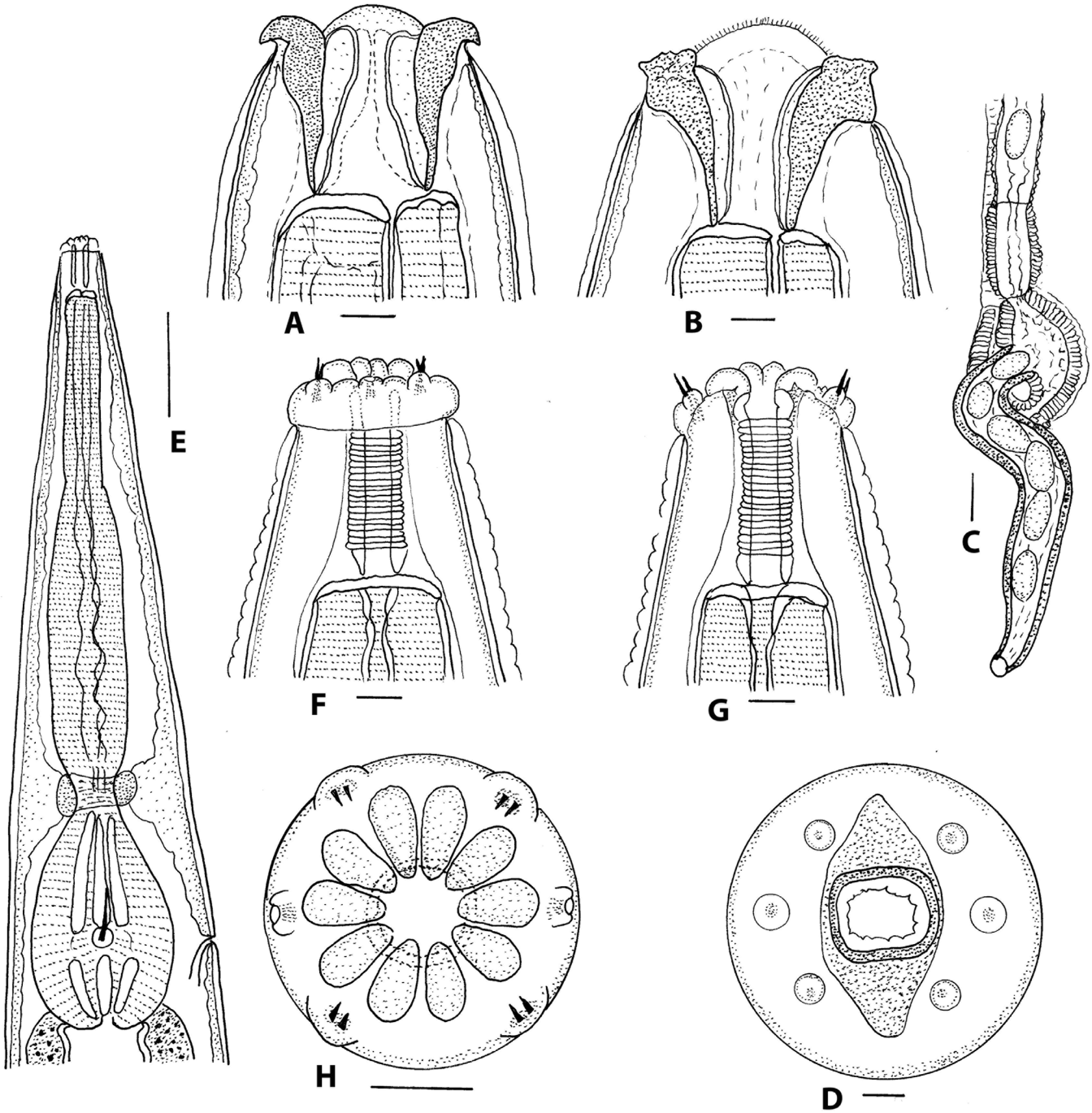


Fig. 30. Genera *Papillostrongylus*, *Pararugopharynx*. A, *Papillostrongylus labiatus*, optical section through buccal capsule lateral view; B, *Papillostrongylus barbatus*, optical section through buccal capsule lateral view; C, *P. barbatus*, vagina, lateral view; D, *P. barbatus*, optical transverse through buccal capsule; E, *Pararugopharynx protemnodontis*, oesophagus, lateral view; F, *Pr. protemnodontis*, buccal capsule, lateral view; G, *Pr. protemnodontis*, optical section through buccal capsule, lateral view; H, *Pr. protemnodontis*, mouth opening, apical view. (A–D from Chilton et al., 2002; E–H from Beveridge, 1998a).

Scale-bars: C, E, 0.1 mm; A, B, D, F–H, 0.01 mm.

***Papillostrongylus labiatus* Johnston & Mawson, 1939**

Papillostrongylus labiatus Johnston & Mawson, 1939a, pp. 143–144, figs 63–68; Skrjabin et al, 1952, p. 296; Popova, 1960, p. 220; Yamaguti, 1961, p. 388; Beveridge, 1986d, pp. 778–779, fig. 1; Beveridge et al., 1998, p. 483; Chilton et al., 2002, pp. 82–85, figs 1–12.

Type data: holotype, allotype, SAM V1559.

Type locality: Eidsvold, Qld. (25° 22'S 151° 7'E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Other hosts: *Notamacropus parryi* (Bennett, 1835); *Osphranter bernardus* (Rothschild, 1904); *Petrogale wilkinsi* Thomas, 1926 (as *Petrogale brachyotis* (Gould, 1841)).

Site in host: stomach.

Distribution: NT (Arnhem Land), eastern Qld, north-eastern NSW. Map: Chilton et al., 2002, p. 88.

Representative DNA sequence data: ITS1, 2: AJ309960.

Diagnostic features (Figs 29 I, J, K, N, Fig. 30 A): Males: 5.6–7.2 mm; females 6.6–8.6 mm; cephalic papillae with single seta; leaf crowns absent; mouth–opening dorso–ventrally elongate; spicules 1.10–1.12 mm in specimens from *N. dorsalis*; 1.19–1.61 mm in specimens from Northern Territory; ovejector J-shaped.

Comments: Chilton et al. (2002) noted that population in the Northern Territory was highly disjunct geographically compared with the population on the east coast of Australia and differed in spicule lengths suggesting the existence of an independent species. In eastern Australia, *N. dorsalis* is the primary host of this nematode species with its occurrence in *N. parryi* being uncommon (Beveridge et al., 1998). The parasite has not been found in *N. rufogriseus*. The record in Spratt & Beveridge (2016, p. 143) is an error and the specimen in question is *Pop. wallabiae* (see Chilton et al., 2002). Chilton et al. (2002) included *Thyl. thetis* as a host, but this specimen was referred to as *Papillostrongylus* sp. by Spratt & Beveridge (2016). Its identification warrants further investigation.

Paralabiostrongylus Smales, 1982

Type species: *Pl. bicollaris* Smales, 1982.

Other species: *Pl. rajempatensis* Purwaningsih & Smales, 2014; *Pl. tuberis* Purwaningsih & Smales, 2018.

Generic definition: anterior end with 2 prominent cervical collars; cephalic collar present; cephalic papillae conical, with single seta, not on lips; 6 fleshy lips with prominent pulp cavity; amphids on bases of lateral lips; buccal capsule wider than long, non-striated; oesophagus clavate; diverticula present at oesophago-intestinal junction; deirid, nerve ring and excretory pore in anterior oesophageal region; bursa without bosses on surface; external branchlets of dorsal ray arising at or anterior to principal bifurcation, shorter than parallel, internal branchlets; spicules elongate, alate; gubernaculum present; ovejector J-shaped.

Key to species of Paralabiostrongylus

1a. Dorsal lobe of bursa only slightly longer than lateral lobes; external branchlets of dorsal ray arising immediately anterior to principal bifurcation (Fig. 31 D) . . . . . *Pl. bicollaris*

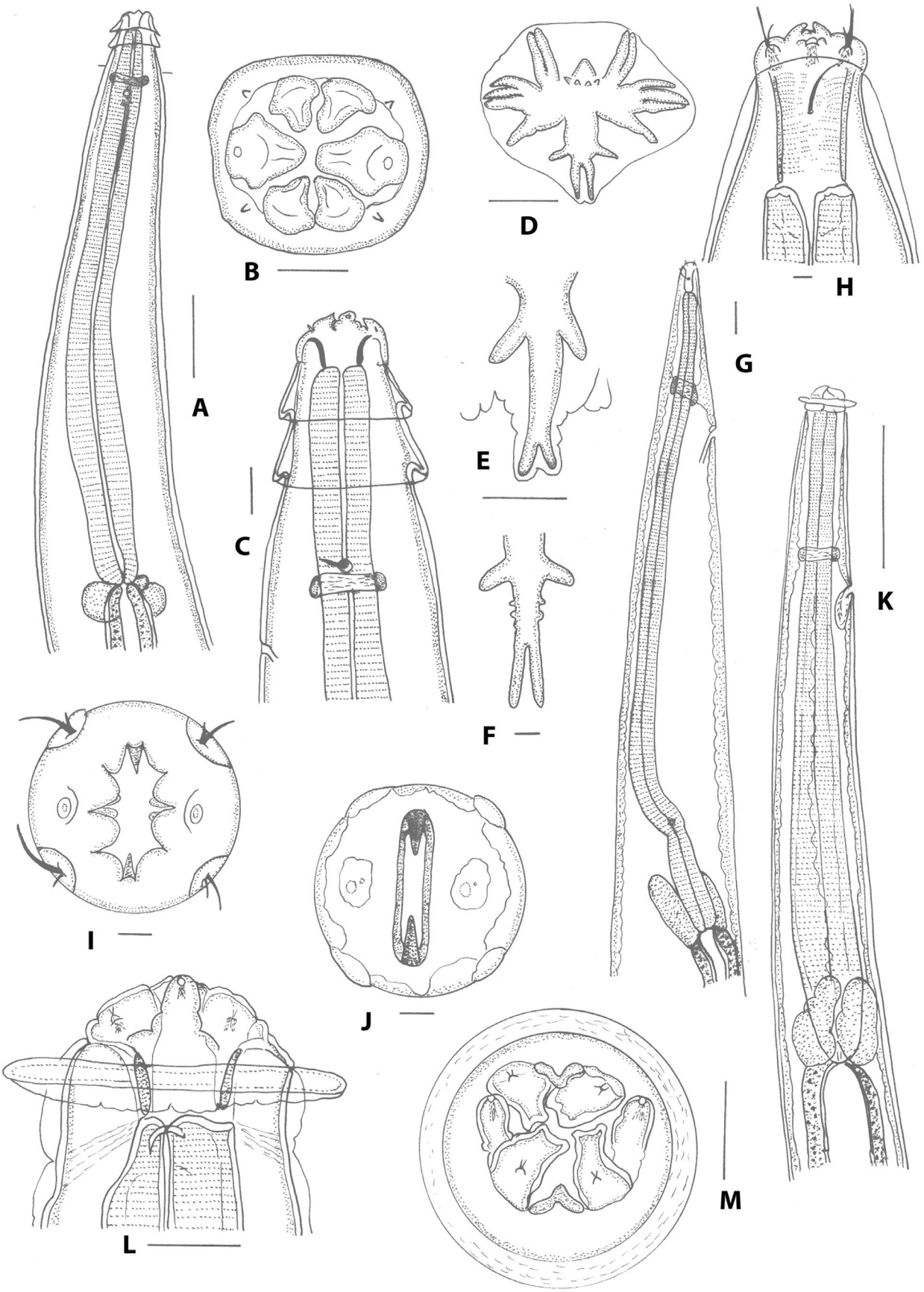
1b. Dorsal lobe of bursa much longer than lateral lobes; external branchlets of dorsal ray arising well anterior to principal bifurcation (Figs 31 E, F) 2

2a. Deirids immediately anterior to nerve ring; dorsal ray without lateral protuberances (Fig. 31 E) . . . . . *Pl. rajempatensis*

2b. Deirids immediately posterior to nerve ring; dorsal ray usually with small lateral protuberances (Fig. 31 F) . . . . . *Pl. tuberis*

Fig. 31. Genera *Paralabiostrongylus*, *Parapharyngostrongylus* and *Parazoniolaimus*. A, *Paralabiostrongylus bicollaris*, oesophagus, lateral view; B, *Pl. bicollaris*, mouth opening, apical view; C, *Pl. bicollaris*, anterior end, lateral view; D, *Pl. bicollaris*, bursa; E, *Paralabiostrongylus rajempatensis*, dorsal ray of bursa; F, *Paralabiostrongylus tuberis*, dorsal ray of bursa; G, *Parapharyngostrongylus dentatus*, oesophagus, lateral view; H, *Pp. dentatus*, buccal capsule, lateral view; I, *Pp. dentatus*, mouth opening, apical view; J, *Pp. dentatus*, optical transverse section through anterior region of buccal capsule; K, *Parazoniolaimus collaris*, oesophagus, lateral view; L, *Pz. collaris*, buccal capsule, lateral view; M, *Pz. collaris,* mouth opening, apical view. (A–D from Smales, 1982a; E, F, from Purwaninsih & Smales, 2014, 2018; G–J from Beveridge, 1998a; K–M, original).

Scale-bars: A, D, 0.5 mm; B, 0.05 mm; C, E, G, K–M, 0.1 mm; F, 0.025 mm; H–J, 0.01 mm.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***Paralabiostrongylus bicollaris* Smales, 1982**

Paralabiostrongylus bicollaris Smales, 1982a, pp. 369–371, figs 38–47, Plate 1F; 1999, p. 137, 2006, p. 98; Spratt & Beveridge, 2016, p. 126.

Type data: holotype BMNH 1981.4649, allotype BMNH 1981.4650, paratypes BMNH 1981.4651–4654, SAM AHC 8984.

Type locality: Middle Strickland, PNG (7° 1′S 142° 12′E).

Type host: *Dorcopsis luctuosa* (D'Albertis, 1874) (as *D. veterum* (Lesson, 1827)).

Other hosts: *Dorcopsis hageni* Heller, 1897; *Dorcopsulus vanheurni* (Thomas, 1922).

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 31 A–D): Males 20–22 mm; females 23–25 mm; dorsal lobe of bursa slightly longer than lateral lobes; external branchlets arise immediately anterior to major bifurcation; spicules 1.02–1.50 mm; ovejector J-shaped.

***Paralabiostrongylus rajempatensis* Purwaningsih & Smales, 2014**

Paralabiostrongylus rajempatensis Purwaningsih & Smales, 2014, pp. 594–597, figs 14–26, 29.

Type data: holotype, allotype MZB Na 643, paratypes MZB Na 644.

Type locality: Raja Ampat Island, Western New Guinea (1° 06′S 130° 51′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea .

Diagnostic features (Fig. 31 E): Male 10.8 mm; females 15.7–28.8 mm; deirid at level of nerve ring; dorsal lobe of bursa much longer than lateral lobes; external branchlets arise well anterior to final bifurcation; spicules 1.08 mm; ovejector J-shaped.

Comments: See those for *Pl. tuberis*.

***Paralabiostrongylus tuberis* Purwaningsih & Smales, 2018**

Paralabiostrongylus tuberis Purwaningsih & Smales, 2018, pp. 60–62, 65, figs 2 a–o, 4 c–d, f, h.

Type data: holotype, allotype MZB Na 741, paratypes MZB Na 742.

Type locality: Lengguru, Western New Guinea (1° 06′S 130° 51′E).

Type host: *Dorcopsis muelleri* (Schlegel, 1866).

Site in host: stomach.

Distribution: Western New Guinea.

Diagnostic features (Fig. 31 F): Males 12.3–18.1 mm; females 15.3–24.2 mm; deirid posterior to nerve ring; dorsal lobe of bursa much longer than lateral lobes; external branchlets arise well anterior to final bifurcation, body of dorsal ray with small, lateral protuberances; spicules 1.14–1.38 mm; ovejector J-shaped.

Comments: *Paralabiostrongylus tuberis* is very similar to *Pl. rajempatensis* with both described from the same host species in Western New Guinea. They have been discriminated to date primarily on the basis of measurements, slight differences in the position of the deirids and the presence or absence of small protuberances on the dorsal ray (Purwaningsih & Smales, 2018).

Parapharyngostrongylus Beveridge, 1982

Type and only species: *Par. dentatus* Beveridge, 1982.

Generic definition: Cephalic collar present; cephalic papillae on slight elevations of cuticle, with paired setae; labial collar with labial crown consisting of 4 lateral, petaloid elements arranged in pairs and 4 submedian elements overlapping with lateral elements; mouth opening and buccal capsule dorsoventrally elongate; buccal capsule heavily sclerotized, with numerous transverse striations; dorsal and ventral teeth at anterior end of buccal capsule; oesophageal corpus elongate; oesophageal bulb elongate, sub-cylindrical; deirid in region of buccal capsule; anterior extremity of intestine projects anteriorly with dorsal and ventral lobes enveloping posterior region of oesophageal bulb; bursa without bosses on surface; spicules elongate, alate; gubernaculum present; ovejector J-shaped.

***Parapharyngostrongylus dentatus* Beveridge, 1982**

Parapharyngostrongylus dentatus Beveridge, 1982 pp. 46–47, figs 140–155; Beveridge et al., 1998, p. 482; Beveridge, 2016, p. 211.

Type data: holotype SAM V2167, allotype SAM V2168, paratypes SAM V2169–78, 8206, BMNH 1980.606–609; USNPC 75880.

Type locality: Emu Park, Qld (23° 16′S 150° 50′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Other hosts: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: Qld.

Representative DNA sequence data: ITS1, 2: MG865361.

Diagnostic features (Figs 31 G–J): Males 5.8–7.6 mm, females 7.1–9.2 mm; paired submedian cephalic setae dissimilar in length; buccal capsule dorsoventrally

elongate with one dorsal and one ventral tooth at anterior extremity; wider anteriorly in lateral views, with prominent, irregular transverse striations; deirid at level of buccal capsule; nerve ring and excretory pore in anterior oesophageal region; bursa without sclerotised bosses; spicules 1.80–2.09 mm; ovejector J-shaped.

Comments: A highly distinctive species with a compressed buccal capsule and paired teeth at the entry of the buccal capsule, *Par. dentatus* was described originally from *N. dorsalis* but was subsequently found to be more common in *Wal. bicolor* in north Queensland (Beveridge et al., 1998). In *Wal. bicolor*, it is restricted to this geographical region although the host species extends much further south (Beveridge, 2016).

Pararugopharynx Magzoub, 1964

Type and only species: *Pararugopharynx protemnodontis* Magzoub, 1964

Generic definition: Cephalic collar present; cephalic papillae domed, with short, paired setae; labial collar consisting of 10 rounded elements; buccal capsule elongate, heavily sclerotized, circular in cross section, with numerous transverse striations; oesophageal corpus with anterior narrower and posterior broader regions; oesophageal bulb clavate with six sclerotized plates; deirid in region of oesophageal bulb; nerve ring surrounds oesophageal isthmus; intestinal projections absent; bursa without bosses on surface; spicules elongate, alate; gubernaculum absent; ovejector J-shaped.

Pararugopharynx protemnodontis Magzoub, 1964

Pararugopharynx protemnodontis Magzoub, 1964, pp. 50–51, figs 13–19; Munday & Green, 1972, p.7; Beveridge, 1982, pp. 82–84, figs 280–289; Aussavy et al., 2011; p.16; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 241.

Type data: holotype and allotype SAM V1265, paratypes SAM V1265, SAM AHC 4918.

Type locality: Logan Village, Qld. (27° 46′S 153° 06′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Site in host: stomach.

Distribution: Qld, Vic, south-eastern SA, Tas.

Representative DNA sequence data: ITS1, 2: MG865636.

Diagnostic features (Figs 30 E–H, 45 C): Males 2.6–8.3 mm; females 7.1–10.4 mm; spicules 1.05–2.40 mm; tail long, tapering, 0.55–0.84 mm; vagina extremely long, 1.0–1.7mm.

Comments: This distinctive species is known only from the red-necked wallaby, *Notamacropus rufogriseus*.

Parazoniolaimus Johnston & Mawson, 1939

Type and only species: *Parazoniolaimus collaris* Johnston & Mawson, 1939.

Generic definition: anterior end with prominent, disc-like cervical collar; cephalic collar absent; cephalic papillae conical, with paired setae; six fleshy lips with prominent pulp cavity; cephalic papillae near bases of sub-median lips, amphids at tips of lateral lips; buccal capsule wider than long, non-striated; oesophagus clavate; diverticula present at oesophago-intestinal junction; deirid, nerve ring and excretory pore in anterior oesophageal region; bursa without bosses on surface; external branchlets of dorsal ray arising at or immediately anterior to principal bifurcation; spicules elongate, alate; gubernaculum present; ovejector Y-shaped.

Parazoniolaimus collaris Johnston & Mawson, 1939

Parazoniolaimus collaris Johnston & Mawson, 1939b, pp. 522–524, figs 27–29; 1940a, p. 468; Skrjabin et al., 1952, p. 189; Popova, 1960, pp. 107–108, fig. 71; Yamaguti, 1961, p. 407; Arundel et al., 1977, p. 142; Beveridge et al., 1985, p. 378; Smales, 2002, pp. 184–190, figs 13–31, 2006, pp. 99–100; Aussavy et al, 2011, p. 17; Vendl & Beveridge, 2014, p. 109; Beveridge, 2016, p. 212; Spratt et al., 2017, p. 242.

Type data: holotype, allotype SAM AHC 41372.

Type locality: Lower Hawkesbury, NSW (33° 30′S 151° 10′S).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Other hosts: *Notomacropus parma* (Waterhouse, 1846).

Site in host: stomach.

Distribution: NSW, Vic. Map: Smales, 2002, p. 188.

Representative DNA sequence data: ITS1, 2: FR854222, Y10798.

Diagnostic features (Figs 31K–M): Males 22–26 mm; females 28–34 mm; spicules 5.56–6.30 mm.

Comments: Although this distinctive species is a common parasite of *Wal. bicolor*, there are no specimens to substantiate its occurrence in *N. parma* (Johnston & Mawson, 1940a), leaving this host record unsupported.

Pharyngostrongylus Yorke & Maplestone, 1926

Type species: *Pharyngostrongylus macropodis* Yorke & Maplestone, 1926.

Other species: *Ph. dendrolagi* Beveridge, 1982; *Ph. diversus* Beveridge, 1982; *Ph. eta* Johnston & Mawson, 1939; *Ph. gamma* Johnston & Mawson, 1939; *Ph. iota* Johnston & Mawson, 1939; *Ph. kappa* Mawson, 1965; *Ph. lambda* Mawson, 1965; *Ph. nelsoni* Beveridge, 1982; *Ph. ornatus* Davey & Wood, 1938; *Ph. papillatus* Beveridge, 1982; *Ph. patriciae* Sukee, Beveridge & Jabbar, 2018; *Ph. setosus* Beveridge, 1982; *Ph. sharmani* Beveridge, 1982; *Ph. thylogale* Beveridge, 2016.

Generic definition: Cephalic collar present; cephalic papillae domed, with short, paired setae or single elongate seta (*Ph. sharmani*); labial crown consisting of 4, 8, 12 or 16 petaloid elements; buccal capsule elongate, heavily sclerotized, circular in cross section, with numerous transverse or oblique striations; oesophageal corpus elongate; oesophageal bulb elongate, sub–cylindrical; deirid in region of buccal capsule or occasionally slightly posterior to it; anterior extremity of intestine projects anteriorly with dorsal and ventral lobes enveloping oesophageal bulb; bursa with or without bosses on surface; spicules elongate, alate; gubernaculum present or absent; ovejector J-shaped.

Comments: Many of the species of this genus are identifiable based on the morphology of the buccal capsule and emphasis has therefore been placed on this feature in the illustrations. However, other important characters are the number of leaf crown elements (best shown in apical views of the mouth opening) and the presence or absence of bosses on the surface of the bursa.

Key to species of Pharyngostrongylus

1a. Striations of buccal capsule prominent and oblique (Fig. 32 B) 2
1b. Striations of buccal capsule transverse, prominent, faint or almost absent (Figs 32 C–I) 5

2a. Bursa with numerous sclerotized bosses; 8 elements in labial crown 3
2b. Bursa without sclerotized bosses; 16 elements in labial crown 4

3a. Spicules < 2.0 mm . . . . . *Ph. nelsoni*
3b. Spicules > 2.0 mm . . . . . *Ph. papillatus*
4a. Spicules > 3.0 mm . . . . . *Ph. diversus*
4b. Spicules 1.9–2.9 mm . . . . . *Ph. gamma*
4c. Spicules <1.8 mm . . . . . *Ph. ornatus*

5a. Labial crown with 4 elements, serrated at tips (Figs. 32 E, R) . . . . . *Ph. lambda*
5b. Labial crown with 8 or more elements, not serrated at tips 6

6a. Lateral or all labial crown elements bilobed at tips (Figs 32 O, P) 7
6b. Labial crown elements petaloid, none bilobed at tips (Fig. 32 N) 8

7a. Lateral labial crown elements bilobed at tips (Fig. 32 P); bursa without sclerotized bosses . . . . . *Ph. dendrolagi*
7b. All labial crown elements bilobed at tips (Fig. 32 O); bursa with sclerotized bosses . . . . . *Ph. sharmani*

8a. Posterior region of buccal capsule deviated dorsally; valve-like structures present at posterior end of buccal capsule (Figs 32 C, I) 9
8b. Buccal capsule straight or walls sinuous; valve-like structures absent at posterior end of buccal capsule 10

9a. Buccal capsule with faint transverse striations (Fig. 32 I); labial crown with 12 elements (Fig. 32 N) . . . . . *Ph. thylogale*
9b. Buccal capsule with prominent transverse striations (Fig. 32 C); labial crown with 16 elements . . . . . *Ph. macropodis*

10a. Striations of buccal capsule prominent, regular and widely spaced (Figs 3F, G) 11
10b. Striations of buccal capsule faint, irregular or very close together (Figs 32 D, H) 12

11a. Buccal capsule with 38–50 transverse striations (Fig. 32F) . . . . . *Ph. patriciae*
11b. Buccal capsule with 60–64 transverse striations (Fig. 32 G) . . . . . *Ph. kappa*

12a. Bursa with sclerotised bosses . . . . . *Ph. eta*
12b. Bursa without sclerotized bosses 13

13a. Walls of buccal capsule elongate, parallel (Fig. 32 D); spicules > 2 mm . . . . . *Ph. iota*
13b. Buccal capsule squat, walls sinuous (Fig. 32 L); spicules < 2 mm . . . . . *Ph. setosus*

***Pharyngostrongylus dendrolagi* Beveridge, 1982**

Pharyngostrongylus dendrolagi Beveridge, 1982, pp. 31–32, figs 66–77; Flannery, Martin & Szalay, 1996, p. 187.

Type data: holotype BMNH 1976.43; allotype BMNH 1976.44; paratypes BMNH 1976.45–49, SAM V1819–20.

Type locality: Lumusa, PNG (5° 30′S 144° 05′E).

Type host: *Dendrolagus dorianus* Ramsay,1883.

Other hosts: *Dendrolagus mbaiso* Flannery, Boeadi & Szalay, 1995; *Dendrolagus scottae* Flannery & Seri, 1990.

Site in host: stomach.

Distribution: PNG, Western New Guinea .

Diagnostic features (Figs 32 K, P): Males 6.0–10.2 mm, females 7.4–9.7 mm; buccal capsule with faint transverse striations, deviated towards base, with flap–like valve at posterior end; labial crown with 8 elements, 4 lateral elements subdivided at tips; bursa without sclerotized bosses; spicules 3.70–4.35 mm long; ovejector J-shaped.

Comments: This species is apparently restricted to tree kangaroos in Papua New Guinea and has not been found in tree kangaroos in Australia (Beveridge et al., 1992).

***Pharyngostrongylus diversus* Beveridge, 1982**

Pharyngostrongylus diversus Beveridge, 1982, pp. 22–24, figs 31–39.

Type data: holotype SAM V1704, allotype SAM V1705, paratypes SAM V1706–1713, 7624, BMNH 1979.825–828, USNPC 75131.

Type locality: Niagara Park, NSW (33° 23′S 151° 21′E).

Type host: *Notamacropus parma* (Waterhouse, 1846).

Site in host: stomach.

Distribution: NSW; known only from the type locality.

Diagnostic features: Males 7.1–9.1 mm, females 8.9–10.6; buccal capsule straight, elongate, with prominent oblique striations; labial crown with 16 elements; bursa without sclerotized bosses; spicules 3.10–4.44 mm long; ovejector J-shaped.

Comments: This species is most similar to *Ph. ornatus*, differing significantly in spicule lengths (1.20–1.60 mm in *Ph. ornatus*). Johnston & Mawson (1940c) reported *Ph. gamma* from *N. parma*, but their specimens are no longer extant. They were probably specimens of *Ph. diversus*.

***Pharyngostrongylus eta* Johnston & Mawson, 1939**

Pharyngostrongylus eta Johnston & Mawson, 1939a, pp. 139–140, figs 51–55; Wahid, 1964, pp. 181, 188; Mawson, 1965, pp. 150–151, figs. 17–22; Beveridge, 1982, pp. 39–41, figs. 115–124; Spratt et al., 2017, p. 241.

Rugopharynx eta: Yamaguti, 1961, p. 410.

Type data: holotype and allotype, SAM V1856.

Type locality: Millmerran, Qld (27° 53′S 151° 16′E).

Type host: "*Macropus* sp." (most probably *Notamacropus rufogriseus* (Desmarest, 1817)).

Other hosts: *Notamacropus rufogriseus* (Desmarest, 1817), *Notamacropus parryi* (Bennett, 1835).

Site in host: stomach.

Distribution: Qld, NSW, Tas.

Representative DNA sequence data: ITS1, 2: LT576288–90.

Diagnostic features (Fig. 32 H): Males 6.3–7.4 mm, females 6.4–8.9 mm; buccal capsule straight, moderately elongate, with faint, fine regular, transverse striations; labial crown with 8 elements; bursa with sclerotized bosses; spicules 1.15–1.40 mm; ovejector J-shaped.

Comments: This species has been found in Queensland, New South Wales and Tasmania (Beveridge, 1982; Spratt et al., 2017) but appears to be absent in populations of *N. rufogriseus* from western Victoria (Aussavy et al., 2011; Vendl & Beveridge, 2014). The primary host is *N. rufogriseus* and this is most probably the type host species.

***Pharyngostrongylus gamma* Johnston & Mawson, 1939**

Pharyngostrongylus gamma Johnston & Mawson, 1939a, pp. 134–136, figs 34–39; Johnston & Mawson, 1939b, pp. 516–517; Johnston & Mawson, 1940a, p. 468; Popova, 1958, p. 245; Yamaguti, 1961, p. 408; Beveridge, 1982, pp. 24–26, figs 40–47; Beveridge et al., 1989, p. 482.

Type data: holotype and allotype SAM V1552.

Type locality: Upper Burnett River, Qld (24° 45′S 152° 23′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

Distribution: Qld.

Representative DNA sequence data: ITS1, 2: LT576291.

Diagnostic features (Fig. 32 M): Males 5.7–7.2 mm, females 6.5–8.1 mm; buccal capsule straight, elongate, with prominent oblique striations; labial crown with 16 petaloid elements; bursa without sclerotized bosses; spicules 1.85–2.12 mm; ovejector J-shaped.

Comments: Johnston & Mawson (1939a, b) reported *Ph. gamma* from *N. dorsalis*, *N. parma*, *N. parryi* and *N. rufogriseus*. Some of these collections have since been re-identified, that from *N. parma* as *Ph. diversus*, and that from *N. parryi* as *Ph. ornatus.* No specimens exist from *N. rufogriseus* and extensive collections from this host have not revealed the presence of this species (Beveridge, 1982; Aussavy et al., 2011; Vendl & Beveridge, 2014; Spratt et al., 2017).

***Pharyngostrongylus iota* Johnston & Mawson, 1939**

Pharyngostrongylus iota Johnston & Mawson, 1939b, pp. 514–516, figs 3–4; Popova, 1958, p. 245, fig. 165; Wahid, 1964, pp. 181, 188; Mawson, 1964, pp. 244–245; Beveridge, 1982, pp. 41–43, figs 125–132; Beveridge et al., 1992, p. 365; Griffith et al., 2000, pp. 309, 310.

Rugopharynx iota: Yamaguti, 1961, p. 410; Wahid, 1964, p.188.

Type data: holotype and allotype SAM V1369.

Type locality: Ourimbah, NSW (29° 17′S 143° 39′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817) (probably an error for *Thylogale thetis* (Lesson, 1827).

Other hosts: *Thylogale thetis* (Lesson, 1827); *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: Qld, NSW.

Representative DNA sequence data: ITS1, 2: LT576292, LT576293.

Diagnostic features (Fig. 32 D): Males 5.2–6.7 mm, females 6.1–8.1 mm; buccal capsule straight, elongate, with fine, faint, transverse striations; labial crown with 8 petaloid elements; bursa without sclerotized bosses; spicules 1.15–1.40 (1.27) mm; ovejector J-shaped.

Comments: Based on current collections, this species has not been found in *N. rufogriseus* and it is highly likely that the incorrect host name arose from confusion between the common names "red–necked wallaby" and "red–necked pademelon". Some of the material from *Thyl. stigmatica* identified as *Ph. iota* by Griffith et al. (2000) was subsequently re-identified as *Ph. thylogale* (see Chilton et al., 2016).

***Pharyngostrongylus kappa* Mawson, 1965**

Pharyngostrongylus kappa Mawson, 1965, pp. 147–150, figs 10–16; Beveridge & Arundel, 1979, p. 72; Beveridge, 1982, pp. 37–39, figs 106–114; Arundel et al., 1990, p. 42; Beveridge et al., 1998, p. 482; Aussavy et al., 2011, p. 14; Vendl & Beveridge, 2014, p. 108; Cripps et al., 2015, p. 168; Spratt et al., 2017, p. 240; Sukee et al., 2018, pp. 2–14.

Type data: holotype SAM V1700, allotype SAM V1701, paratypes SAM AHC 4907, 6287.

Type locality: Inglewood, Qld (28° 25′S 151° 05′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Notamacropus rufogriseus* (Desmarest, 1817); *Macropus fuliginosus* (Desmarest, 1817); *Petrogale assimilis* Ramsay, 1877.

Site in host: stomach.

Distribution: Qld, NSW, ACT, Vic, Tas. Map: Sukee et al., 2018, p. 3.

Representative DNA sequence data: ITS1, 2: MG972109–53.

Diagnostic features (Fig. 32 G): Males 5.5–10.0 mm, females 7.1–7.8 mm; buccal capule straight, elongate with 60–64 very prominent, regular, transverse striations; labial crown with 8 petaloid elements; bursa with sclerotized bosses; spicule length 2.20–2.65 mm; ovejector J-shaped.

Comments: *Pharyngostrongylus kappa* is a common and abundant parasite of *Mac. giganteus* (see references above). Occurrences in other hosts are extremely limited. Specimens from *Osphranter robustus*, *O. antilopinus* and *O. bernardus* included in *Ph. kappa* by Beveridge (1982) are now considered to belong to *Ph. patriciae*.

***Pharyngostrongylus lambda* Mawson, 1965**

Pharyngostrongylus lambda Mawson, 1965, pp. 151–152, figs. 23–30; Beveridge, 1982, pp. 28–30, figs. 56–65; Beveridge et al., 1989, p. 277; 1998, p. 482; Lott et al., 2014, p. 78; Beveridge, 2020c, p. 4, 2020e, p. 204.

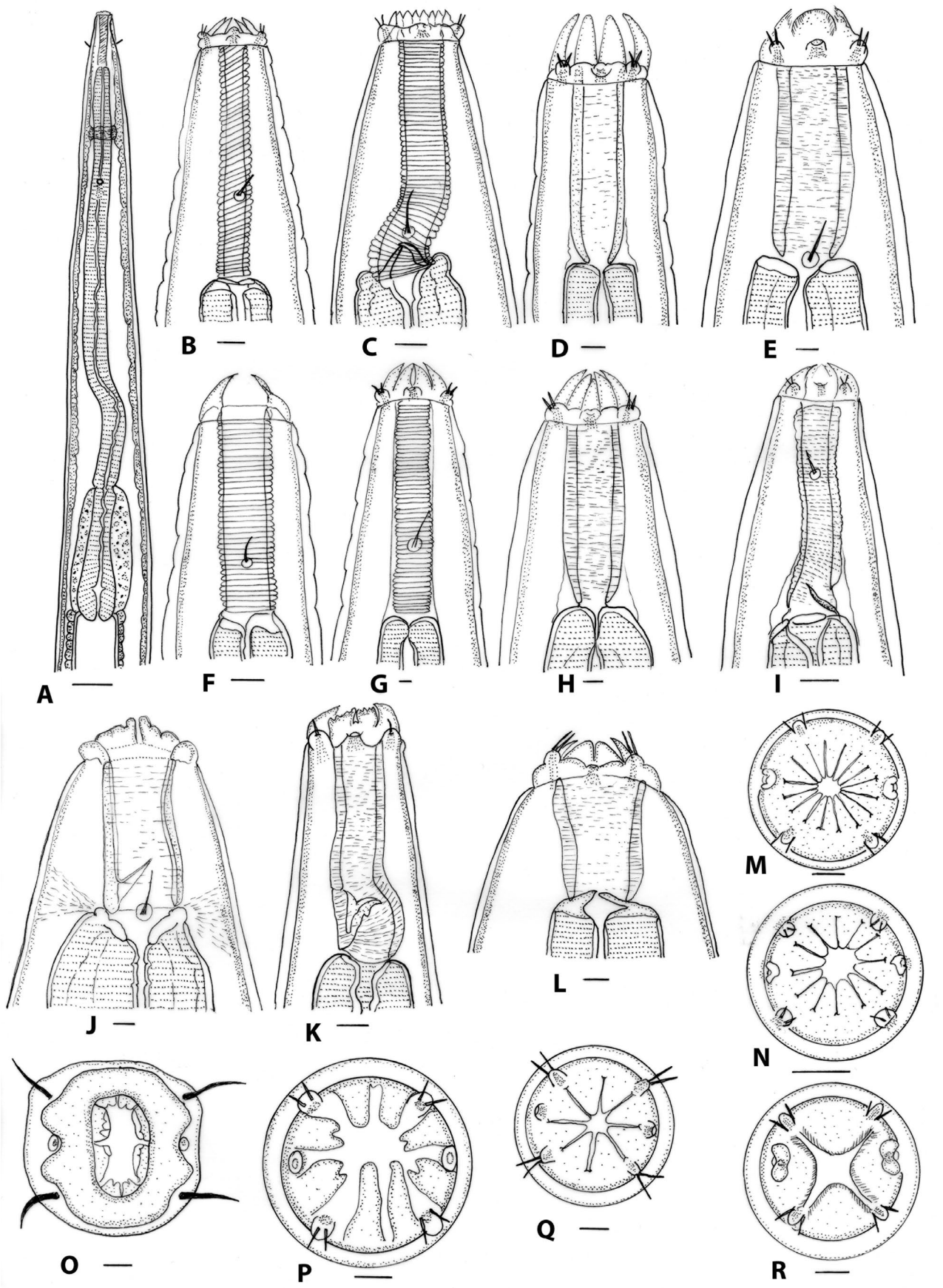
Type data: holotype and allotype SAM V1698.

Type locality: Marble Bar, WA (21° 09′S 199° 44′E).

Type host: *Osphranter robustus* (Gould, 1840).

Fig. 32. Genus *Pharyngostrongylus*. A, *Pharyngostrongylus nelsoni*, anterior end, ventral view; B, *Ph. nelsoni*, buccal capsule, lateral view; C, *Ph. macropodis*, buccal capsule, lateral view; D, *Ph. iota*, buccal capsule, lateral view; E, *Ph. lambda*, buccal capsule, lateral view; F, *Ph. patriciae*, buccal capsule, lateral view; G, *Ph. kappa*, buccal capsule, lateral view; H, *Ph. eta*, buccal capsule, lateral view; I, *Ph. thylogale*, buccal capsule, lateral view; J, *Ph. sharmani*, buccal capsule, lateral view; K, *Ph. dendrolagi*, buccal capsule, lateral view; L, *Ph. setosus*, buccal capsule, lateral view; M, *Ph. gamma*, anterior end, apical view; N, *Ph. thylogale*, anterior end, apical view; O, *Ph. sharmani*, anterior end, apical view; P, *Ph. dendrolagi*, anterior end, apical view; Q, *Ph. setosus*, anterior end, apical view; R, *Ph. lambda*, anterior end, apical view. (A–E, G, H, J–M, O–R, from Beveridge, 1982; F, from Sukee et al., 2018; I, N, from Chilton et al., 2016).

Scale-bars: A, 0.1 mm, B–R, 0.01 mm.


A
B
C
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R

Other hosts: *Macropus giganteus* Shaw, 1790; *Osphranter rufus* (Desmarest, 1822); *Petrogale assimilis* Ramsay, 1877; *Petrogale herberti* Thomas, 1926; *Petrogale purpureicollis* Le Souef, 1924.
Site in host: stomach.
Distribution: Qld, WA.
Representative DNA sequence data: ITS1, 2: LT576297–9, KJ776396.
Diagnostic features (Figs 32 E, R): Males 9.3–11.5 mm, females 10.5–14.2 mm; buccal capsule straight, elongate with fine, irregular transverse striations; labial crown with 4 elements; margins of labial crown elements serrated; bursa with sclerotized bosses; spicules 1.65–1.90 mm; ovejector J-shaped.
Comments: This species is a common parasite of *O. robustus, O. rufus* and *Mac. giganteus* in northern Australia (Beveridge et al., 1998; Beveridge, 2020e) and an uncommon parasite of rock wallabies (*Petrogale* spp.) (Beveridge et al., 1989). The species is readily recognisable by its serrated labial crown elements.

***Pharyngostrongylus macropodis* Yorke & Maplestone, 1926**

Pharyngostrongylus macropodis Yorke & Maplestone, 1926, p. 65–67, fig. 34; Johnston & Mawson, 1939a, pp. 121, 134, 140; 1939b, pp. 513, 517; Popova, 1958, p. 236, fig. 159; Yamaguti, 1961, p. 408, fig. 491; Wahid, 1964, pp. 181–184, figs 1, 6; Mawson, 1965, pp. 146–147, figs 1–9; Beveridge, 1982, pp. 34–37, figs 10, 83–105; Speare et al., 1983, p. 90; Beveridge et al., 1998, p. 482.
Type data: syntypes BMNH 1927.7.21.9–12.
Type locality: Townsville, Qld (19° 15′S 146° 49′E).
Type host: *Notamacropus agilis* (Gould, 1842) (as *Macropus* sp. in original publication).
Other hosts: *Notamacropus parryi* (Bennett, 1835): *Notamacropus rufogriseus* (Desmarest, 1817); *Osphranter antilopinus* (Gould, 1842); *Petrogale godmani* Thomas, 1923; *Petrogale wilkinsi* Thomas, 1926 (as *P. venustula* Thomas, 1926).
Site in host: stomach.
Distribution: NT, Qld.
Representative DNA sequence data: ITS1, 2: LT576300.
Diagnostic features (Fig. 32 C): Males 8.9–12.5 mm, females 13.3–15.7 mm; buccal capsule elongate with prominent basal deviation and prominent transverse striations; paired flap-like valves at posterior end of buccal capsule; labial crown with 16 petaloid elements; bursa with sclerotized bosses; spicules 1.88–2.10 mm long; ovejector J-shaped.
Comments: *Pharyngostrongylus macropodis* is a common parasite of *N. agilis* and also occurs in *N. parryi* where the two species occur in sympatry (Beveridge et al., 1998). Its occurrence in other host species is extremely limited.

***Pharyngostrongylus nelsoni* Beveridge, 1982**

Pharyngostrongylus nelsoni Beveridge, 1982, pp. 19–22, figs 22–30.
Type data: holotype SAM V1726, allotype SAM V1727, paratypes SAM V1728–1747, BMNH 1979.815–824, USNPC 75130.
Type locality: Mount Borradaile, NT (12° 03′S 132° 54′E).
Type host: *Petrogale wilkinsi* Thomas, 1926 (as *P. venustula* Thomas, 1926).
Other hosts: *Osphranter bernardus* (Rothschild, 1904).
Site in host: stomach.
Distribution: Arnhem Land, NT.
Diagnostic features (Figs 32 A, B): Males 5.3–7.0 mm, females 6.5–7.7 mm; buccal capsule, straight, elongate, with prominent oblique striations; labial crown with 8 petaloid elements; bursa with sclerotized bosses; spicules 1.48–1.74 mm; ovejector J-shaped.
Comments: This species is known only from wallaroos and rock wallabies in Arnhem Land, NT.

***Pharyngostrongylus ornatus* Davey & Wood, 1938**

Pharyngostrongylus ornatus Davey & Wood, 1938, pp. 264–266, figs 11–12; Johnston & Mawson, 1939c, p. 209; Popova, 1958, pp. 247–248, fig. 161; Yamaguti, 1961, p. 408; Wahid, 1964, pp. 181–184, fig. 5; Beveridge, 1982, pp. 26–28, figs 48–55; Beveridge et al., 1998, p. 482.
Type data: syntypes BMNH 1939.1.10.135–137; QM GL 12154.
Type locality: Yabulu, Qld (19° 12′S 146° 36′E).
Type host: *Osphranter robustus* (Gould, 1840) (as *Macropus robustus* Gould, 1840).
Other hosts: *Notamacropus parryi* (Bennett, 1835).
Site in host: stomach.
Distribution: Qld.
Representative DNA sequence data: ITS1, 2: LT576302–3.
Diagnostic features: Males 6.0–8.3 mm, females 7.2–8.5 mm; buccal capsule straight, elongate with prominent oblique striations; labial crown with 16 petaloid elements; bursa without sclerotized bosses; spicules 1.20–1.60 mm; ovejector J-shaped.
Comments: The type and only host is considered to be *N. parryi* as *Ph. ornatus* has not been found in *O. robustus* since the original description (Beveridge, 2020c). The original name of the type host is apparently an error. The same apparent error occurs in the case of *Macropostrongylus macrostoma*.

***Pharyngostrongylus papillatus* Beveridge, 1982**

Pharyngostrongylus papillatus Beveridge, 1982, pp. 17–19, figs 14–21; Beveridge et al., 1998, p. 482; Sukee et al., 2018, p. 4; Beveridge, 2020c, p. 4.

Type data: holotype SAM V1714, allotype SAM V1715, paratypes SAM V1716–1725.

Type locality: 80 km SW of Darwin, NT (13° 07′S 130° 30′E).

Type host: *Osphranter antilopinus* (Gould, 1842).

Other hosts: *Osphranter robustus* (Gould, 1840); *Osphranter bernardus* (Rothschild, 1904).

Site in host: stomach.

Distribution: WA, NT, Qld.

Representative DNA sequence data: ITS1, 2: LT576304, MG 519827–8, 972188–9.

Diagnostic features: Males 6.1–9.3 mm, females 9.6–11.1 mm; buccal capsule straight, elongate with prominent oblique striations; labial crown with 8 petaloid elements; bursa with sclerotized bosses; spicules 2.20–2.80 mm; ovejector J-shaped.

Comments: This species is restricted to *O. antilopinus, O. bernardus* and *O. robustus* in northern Australia.

***Pharyngostrongylus patriciae* Sukee, Beveridge & Jabbar, 2018**

Pharyngostrongylus patriciae Sukee, Beveridge & Jabbar, 2018, p. 6, fig. 3.

Type data: holotype SAM 48125, allotype SAM 48126, paratypes SAM 48127.

Type locality: Pine Creek, NT (15° 44′S 136° 06′S).

Type host: *Osphranter robustus* (Gould, 1840).

Other hosts: *Osphranter antilopinus* (Gould, 1842); *Osphranter bernardus* (Rothschild, 1904).

Site in host: stomach.

Distribution: NT, Qld, WA. Map: Sukee et al., 2018, p. 3.

Representative DNA sequence data: ITS1, 2: MG972155–69.

Diagnostic features (Fig. 32 F): Males 5.6–7.9 mm, females 7.2–10.3 mm; buccal capule straight, elongate with 38–50 very prominent transverse striations; labial crown with 8 petaloid elements; bursa with sclerotized bosses; spicule length 1.98–2.25 mm; ovejector J-shaped.

Comments: This species was formerly confused with *Ph. kappa*, but can be differentiated based on morphological features of the buccal capsule as well as molecular criteria. The buccal capsule of *Ph. patriciae* is shorter than that of *Ph. kappa* and has 38–50 transverse striations compared with 60–64 in *Ph. kappa*. *Pharyngostrongylus patriciae* appears to be restricted to species of *Osphranter*.

***Pharyngostrongylus setosus* Beveridge, 1982**

Pharyngostrongylus setosus Beveridge, 1982, pp. 44–45, figs 133–139; Beveridge et al., 1992, p. 365; Griffith et al., 2000, p. 310.

Type data: holotype SAM V1748, allotype SAM V1749, paratypes SAM V1750–1757, BMNH 1979. 829–830, USNPC 75132.

Type locality: El Arish, Qld (17° 49′S 146° 00′E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: Qld.

Representative DNA sequence data: ITS1, 2: LT576305.

Diagnostic features (Figs 32 L, Q): Males 4.8–8.1 mm, females 7.4–9.1 mm; buccal capsule short, with fine, irregular transverse striations, walls sinuous; labial crown with 8 petaloid elements; bursa without sclerotised bosses; spicules 1.33–1.46 mm; ovejector J-shaped.

Comments: This species appears to be restricted to *Thyl. stigmatica* in north-eastern Queensland.

***Pharyngostrongylus sharmani* Beveridge, 1982**

Pharyngostrongylus sharmani Beveridge, 1982, pp. 32–34, figs 75–82; Sukee et al., 2018, pp. 4, 11, 13–14.

Type data: holotype SAM V2139, allotype SAM V2140, paratypes SAM V2141–2160, SAM AHC 8230, BMNH 1980.601–604, USNPC 75878.

Type locality: El Sharanah, NT (13° 31′S 132° 31′E).

Type host: *Osphranter bernardus* (Rothschild, 1904).

Other hosts: *Osphranter antilopinus* (Gould, 1842); *Osphranter robustus* (Gould, 1840).

Site in host: stomach,

Distribution: NT, WA.

Representative DNA sequence data: ITS1, 2: LT576306, MG972190–1.

Diagnostic features (Figs 32 J, O): Males 7.3–9.6 mm, females 8.5–11.3 mm; buccal capsule short, with faint, irregular transverse striations, dorso-ventrally elongate; cephalic papillae with single elongate seta; labial crown of 8 elements, each bilobed at tip, lateral elements much larger that sub-median elements; single flap-like valve at posterior end of buccal capsule; bursa with sclerotized bosses; spicules 2.12–2.66 mm; ovejector J-shaped.

Comments: This distinctive species, characterised by its bilobed labial crown elements and ventral valve at the posterior end of the buccal capsule, is restricted to wallaroos (*Osphranter* spp.) in northern Australia.

***Pharyngostrongylus thylogale* Beveridge, 2016**

Pharyngostrongylus thylogale Beveridge, 2016 in Chilton et al., 2016, pp. 752–754, figs 1–12.

Pharyngostrongylus iota (in part): Beveridge, 1982; Beveridge et al., 1992; Griffith et al., 2000.

Type data: holotype SAM 33454, allotype SAM 47562, paratypes SAM 36132–4.

Type locality: Tully, Qld (17° 56'S 145° 55'E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: Qld, NSW, PNG.

Representative DNA sequence data: ITS1, 2: LT576307.

Diagnostic features (Figs 32 I, N, 45 D): Males 6.3–8.65 mm, females 7.2–10.3 mm; buccal capsule elongate, slightly deviated at posterior end, with very faint irregular transverse striations; single flap-like valve at posterior end on buccal capsule; labial crown of 12 petaloid elements; bursa with sclerotized bosses; spicules 2.4–2.8 mm; ovejector J-shaped.

Comments: *Pharyngostrongylus thylogale* has been confused with *Ph. iota* in the past and occurs in the same host species. It differs from *Ph. iota* in having a flap-like valve in the buccal capsule and in having sclerotized bosses on the bursa. The species is limited to *Thyl. stigmatica* in eastern Australia and Papua New Guinea.

Popovastrongylus Mawson, 1977

Type species: *Pop. wallabiae* (Johnston & Mawson, 1939).

Other species: *Pop. irma* Mawson, 1977; *Pop. macropodis* Beveridge, 1986; *Pop. pearsoni* (Johnston & Mawson, 1940); *Pop. pluteus* Smales, 2000; *Pop. tasmaniensis* Smales, 2000; *Pop. thylogale* Beveridge, 1986.

Species inquierenda: *Pop. medioannulatus* (Johnston & Mawson, 1940).

Generic diagnosis: Cephalic and labial collars present; cephalic papillae with pair of setae; mouth opening sub-circular to quadrangular; leaf crowns absent; buccal capsule with outer sclerotized region, sometimes striated, and inner, transparent lining sometimes forming shelf; oesophageal corpus cylindrical; isthmus indistinct or elongate; bulb ovoid without sclerotized plates; nerve ring in region of isthmus or in anterior oesophageal region; excretory pore roughly at level of nerve ring; deirid in anterior oesophageal region; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum present or absent; ovejector J-shaped.

Comments: The descriptions of several species of *Popovastrongylus* are incomplete and earlier specific differentiations have in some cases been based on incorrect descriptions (Beveridge, 1986b; Smales, 1997b, 2000). A comprehensive review of this genus is necessary to confirm the validity of some of the species described here.

Key to species of Popovastrongylus

Comment: *Pop. medioannulatus* has not been included as its description is too poor and is considered to be a *species inquirenda*.

1a. Buccal capsule with prominent transverse striations (Fig. 33 B) . . . . . *Pop. thylogale*

1b. Buccal capsule without prominent transverse striations 2

2a. Inner lining of buccal capsule forming prominent shelf (Figs 33 E, F) 3

2b. Inner lining of buccal capsule not forming prominent shelf 4

3a. Nerve ring surrounds oesophageal corpus anterior to isthmus . . . . . *Pop. pluteus*

3b. Nerve ring surrounds oesophagus at anterior end of isthmus . . . . . *Pop. pearsoni*

4a. Anterior intestine enveloping oesophageal bulb (Fig. 33 H) . . . . . *Pop. tasmaniensis*

4b. Anterior intestine not enveloping oesophageal bulb 5

5a. Buccal capsule wider than long (Fig. 33 I) *Pop. irma*

5b. Buccal capsule longer than wide. 6

6a. Oesophageal bulb and isthmus 1/7th–1/8th of total oesophageal length (Fig. 33 D) . *Pop. macropodis*

6b. Oesophageal bulb and isthmus 1/3rd–1/4th of total oesophageal length . . . *Pop. wallabiae*

***Popovastrongylus irma* Mawson, 1977**

Popovastrongylus irma Mawson, 1977b, pp. 57–58, figs 34–40.

Type data: holotype SAM AHC 41671, allotype SAM AHC 41672.

Type locality: Perth, WA (31° 57'S 115° 51'E).

Type host: *Notamacropus irma* (Jourdan, 1837).

Site in host: stomach.

Distribution: south-western WA.

Diagnostic features (Fig. 33 I): Males 8.7–10.1 mm; females 11.1–13.0 mm; buccal capsule wider than long, with sclerotised ring at mid-length; shelf absent; oesophagus 1.19–1.30 (male), 1.40–1.58 (female) mm; nerve ring 0.72–0.85 (m), 0.88–0.97 (f), excretory pore 0.9–1.0 (m), 0.98–1.10 (f), deirid 0.19–0.24 (m), 0.24–0.27 (f) mm from anterior end; nerve ring surrounds oesophagus at anterior extremity of isthmus; spicules 1.10–1.40 mm; tail 0.25–0.40 mm; vulva to posterior end 0.59–0.77 mm; female tail swollen; ovejector J-shaped.

Comments: This species is poorly known and warrants redescription. The additional measurements for the type series provided here were made by P.M. Mawson but were not published.

***Popovastrongylus macropodis* Beveridge, 1986**

Popovastrongylus macropodis Beveridge, 1986b, pp. 258–260, figs 1A–M; Beveridge et al., 1998, p. 483; Spratt & Beveridge, 2016, p. 135; Beveridge, 2020c, p. 6, 2020e, p. 204.

Type data: holotype SAM V3632, allotype SAM V3633, paratypes SAM AHC 13378–9.

Type locality: Pallamana Station via Charters Towers, Qld (21° 31′S 146° 32′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Notamacropus agilis* (Gould, 1842) (captive host); *Notamacropus parryi* (Bennett, 1835); *Osphranter robustus* (Gould, 1840); *Osphranter rufus* (Desmarest, 1822).

Site in host: stomach.

Distribution: Qld.

Representative DNA sequence data: ITS1, 2: MG865633.

Diagnostic features (Figs 33 C, D): Male 7.8 mm; females 7.4–8.8 mm; buccal capsule longer than wide, sclerotised region elongate, widest at mid-length; shelf absent from buccal capsule; oesophageal corpus very long; nerve ring surrounds oesophagus in anterior oesophageal region; spicules 1.01 mm; ovejector J-shaped.

***Popovastrongylus medioannulatus* (Johnston & Mawson, 1940) sp. inq.**

Cyclostrongylus medioannulatus Johnston & Mawson, 1940a, p. 471, fig. 13; Popova, 1960, p.80, fig. 50; Skrjabin et al, 1952, p. 176; Yamaguti, 1961, p. 408.

Popovastrongylus medioannulatus: Mawson, 1977b, p. 19; Smales, 1997b, p. 165.

Type data: SAM AHC 27863 (slide).

Type locality: Burnett River, Qld. (25° 03′S 152° 02′E).

Type host: *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: Qld.

Diagnostic features: Female 5 mm; cephalic papillae with paired setae; buccal capsule wider than long; slerotised annulus in mid region of buccal capsule.

Comments: This species is extremely poorly known. It has not been reported in *T. thetis* since its original description (Griffith et al., 2000) but is most similar to *Pop. thylogale* according to Smales (1997b). Smales (1997b) cited the AHC number as 2660, but this is a specimen of *Zoniolaimus buccalis* and it is likely that the material referred to in her paper is AHC 2666, although this is a wet specimen, not a slide. SAM AHC 27863 is designated as the type material in the SAM database and is a slide. This slide was re-examined and consists mainly of unidentifiable fragments of nematodes, but there is one anterior end which clearly indicates that it belongs in *Popovastrongylus*. Consequently, it is treated here as a *species inquirenda*.

***Popovastrongylus pearsoni* (Johnston & Mawson, 1940)**

Macropostrongylus pearsoni Johnston & Mawson, 1940b, pp. 98–99, figs 6–8; Skrjabin et al, 1952, p. 292; Yamaguti, 1961, p. 385; Popova, 1958, p. 257; Mawson, 1971, pp. 171–173, figs 9–13; Smales & Mawson 1978a, pp. 11, 12, 1978b, p. 80.

Popovastrongylus pearsoni: Mawson, 1977b, pp. 56–57, figs 31–33, 48; Beveridge 1986b, pp. 263–264, figs 3A–F; Pamment et al., 1994, p. 191; Webley et al., 2004, p. 625; Aussavy et al., 2011, pp. 14,15; Cripps et al., 2015, p. 168; Spratt & Beveridge, 2016, p. 147; Beveridge, 2020e, p. 204.

Type data: "types" SAM AHC 41377.

Type locality: Pearson Island, SA (33° 58′S 134° 17′E).

Type host: *Petrogale lateralis pearsoni* Thomas, 1922.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817); *Macropus giganteus* Shaw, 1790; *Notamacropus eugenii* (Desmarest, 1817); *Notamacropus rufogriseus* (Desmarest, 1817); *Osphranter robustus* (Gould, 1840); *Osphranter rufus* (Desmarest, 1822).

Site in host: stomach.

Distribution: SA, Vic, Tas.

Representative DNA sequence data: ITS1, 2: MG865634–5.

Diagnostic features (Fig. 33 E): Males 5.7–6.5 mm; females 6.9–7.3 mm; mouth opening quadrangular; labial collar striated; buccal capsule slightly longer than wide; sclerotised section elongate, thickest in posterior half of capsule; internal lining of buccal capsule forming distinct shelf; oesophagus short, nerve ring at

anterior end of narrower isthmus; spicules 0.94–1.01 mm; ovejector J-shaped.

Comments: This species has a wide geographical and host species range in south-eastern Australia.

***Popovatrongylus pluteus* Smales, 2000**

Popovastrongylus pluteus Smales, 2000, pp. 55–57, figs 22–31; Beveridge, 2020c, p. 6.

Type data: holotype SAM AHC 31253, allotype SAM AHC 31324, paratypes SAM AHC 14546, 31252.

Type locality: Rivertree, NSW (28º 37'S 152º 15'E).

Type host: *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Distribution: north-eastern NSW.

Diagnostic features (Fig. 33 F): Males 5.0–6.0 mm; females 7.0–8.0 mm; mouth opening circular; labial collar striated; buccal capsule slightly longer than wide; sclerotised section elongate, thickest in posterior half of capsule; internal lining of buccal capsule forming distinct shelf; oesophagus short, nerve ring in anterior oesophageal region; spicules 0.95 mm; ovejector J-shaped.

***Popovastrongylus tasmaniensis* Smales, 2000**

Popovastrongylus tasmaniensis Smales, 2000, pp. 52–54, figs 7–21.

Type data: holotype SAM AHC 31310, allotype SAM AHC 31311, paratypes SAM AHC 19844.

Type locality: Launceston, Tas (41º 27'S 147º 10'E).

Type host: *Thylogale billardierii* (Desmarest, 1822).

Site in host: stomach.

Distribution: Tas.

Representative DNA sequence data: ITS1, 2: MG865636.

Diagnostic features (Fig. 33 H): Males 6.5–9.0 mm; females 8.0–10.0 mm; mouth opening oval; labial collar not striated; buccal capsule slightly longer than wide; sclerotised section elongate, thickest in posterior half of capsule; internal lining of buccal capsule not forming distinct shelf; oesophagus short; anterior part of intestine surrounds oesophageal bulb; nerve ring in anterior oesophageal region; spicules 1.16–1.45 mm; ovejector J-shaped.

***Popovastrongylus thylogale* Beveridge, 1986**

Popovastrongylus thylogale Beveridge, 1986b, pp. 260–263, figs 2A–L; Beveridge et al., 1989, p. 277, 1992, p. 364; Begg et al., 1995, p. 47; Griffith et al., 2000, p. 310; Spratt & Beveridge, 2016, p. 261.

Type data: holotype SAM V3639, allotype SAM V3640, paratypes SAM V3641–4, SAM AHC 12350, MNHNP 553HD.

Type locality: Wongabel State Forest, Qld. (17º 20'S 145º 29'E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Petrogale persephone* Maynes, 1982; *Thylogale browni* (Ramsay, 1877) (as *T. brunii* (Schreber, 1778)); *Thylogale calabyi* Flannery, 1992; *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: eastern Qld, PNG.

Representative DNA sequence data: ITS1, 2: MG865638.

Diagnostic features (Figs 33 A, B): Males 5.0–5.8 mm; females 6.2–6.4 mm; labial collar striated; mouth opening pentagonal; buccal capsule wider than long; sclerotized region extends full length of buccal capsule, widest in mid-region, with prominent transverse striations; shelf lacking in buccal capsule; nerve ring at anterior extremity of elongate oesophageal isthmus; spicules 0.90–0.96 mm; ovejector J-shaped.

Comments: This nematode is primarily a parasite of *Thylogale* spp. but also occurs in *Pet. persephone* which is sympatric with *Thyl. stigmatica*. However, Chilton et al. (2018) noted genetic differences between specimens from these two host species suggesting that additional investigations are warranted.

***Popovastrongylus wallabiae* (Johnston & Mawson, 1939)**

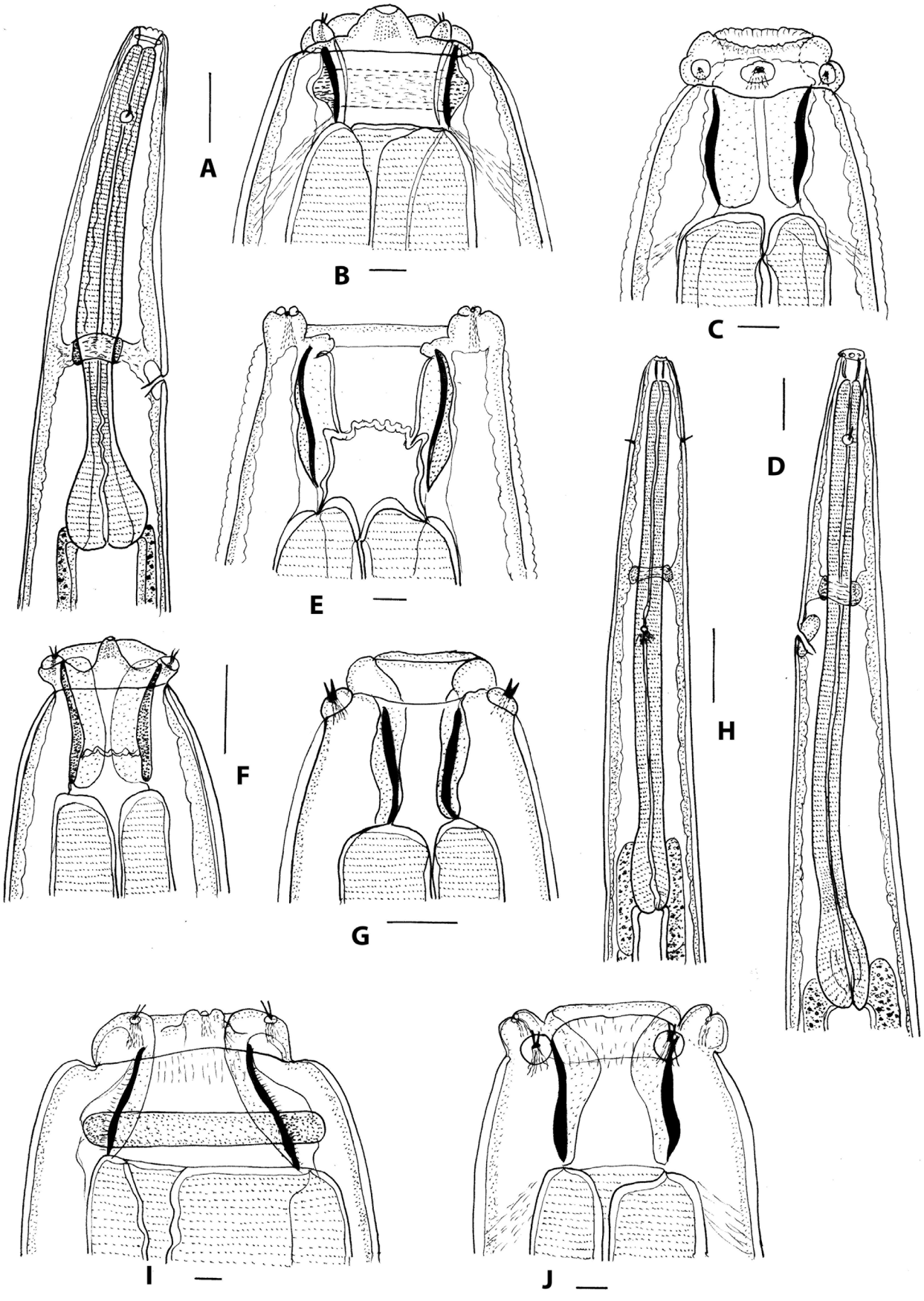
Macropostrongylus wallabiae Johnston & Mawson, 1939b, pp. 525–526, fig. 33; Skrjabin et al, 1952, p. 174; Yamaguti, 1961, p. 408.

Gelanostrongylus wallabiae: Popova, 1960, pp. 89–90, fig. 58.

Popovastrongylus wallabiae: Mawson, 1977b, p. 56, figs 25–30, 49; Smales, 2000, p. 52, figs 1–8; Spratt & Beveridge, 2016, p. 166 (captive host).

Fig. 33. Genus *Popovastrongylus*. A, *Popovastrongylus thylogale*, anterior end lateral view; B, *Pop. thylogale,* buccal capsule, lateral view; C, *Popovastrongylus macropodis*, buccal capsule, lateral view; D, *Pop. macropodis*, anterior end lateral view; E, *Popovastrongylus pearsoni*, buccal capsule, lateral view; F, *Popovastrongylus pluteus*, buccal capsule, lateral view; G, *Popovastrongylus tasmaniensis*, anterior end lateral view; H, *Pop. tasmaniensis*, anterior end lateral view; I, *Popovastrongylus irma*, buccal capsule, lateral view; J, *Popovastrongylus wallabiae*, buccal capsule, lateral view. (A–E, from Beveridge, 1986b; F–H, J from Smales, 2000; I, original).

Scale-bars: A, D, 0.1 mm; B, C, E, H, I, 0.01 mm; F, G, 0.025 mm; H, 0.2 mm.


A
B
C
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J

Type data: holotype, allotype SAM V2842.
Type locality: Bathurst, NSW (33º 25'S 149º 35'E).
Type host: *Notamacropus rufogriseus* (Desmarest, 1817).
Other hosts: *Thylogale thetis* (Lesson, 1827); *Thylogale stigmatica* (Gould, 1860); *Wallabia bicolor* (Desmarest, 1804) (captive host).
Site in host: stomach.
Distribution: eastern Qld, eastern NSW, Tas.
Diagnostic features (Fig. 33 J): (measurements from Johnston & Mawson, 1939b followed by those of Smales, 2000 in brackets): Males 5.5, 8.4 [6.0–9.5] mm; female 7.1–11.4 [10] mm; buccal capsule longer than wide; sclerotized component extends for full length of buccal capsule; internal lining, wider anteriorly, without distinct shelf in mid-region; nerve ring in mid-region of oesophageal corpus; oesophagus 0.95 (male), 1.02–1.12 mm (female) [1.00–1.09 (male), 1.02–1.08 (female)]; nerve ring 0.48 (m), 0.51–0.53 (f) [0.40–0.48 (m), 0.45–0.54 (f)], excretory pore 0.52 (m), 0.50–0.55(f) [0. 48–0.64(m), 0.61–0.64 (f)], deirid 0.28(m), 0.19–0.25(f) [0.23–0.33 (m), 0.28–0.32 (f)] mm from anterior end; spicules 0.61, 0.80 [0.75–0.89] mm; female tail 0.39–0.44 [0.48–0.66] mm; vulva to posterior end 0.65–0.70 [0.75–0.89]; ovejector J–shaped.
Comment: The measurements provided are from the original description as well as additional measurements made by P.M. Mawson but which were not published. The additional measurements were from nematodes collected from *N. rufogriseus* at Logan Village, Qld (Mawson, 1977b). Smales (2000) describing new material from Tasmania, corrected several errors in earlier descriptions. Because of the lack of metric data, her measurements have also been added.

Potorostrongylus Johnston & Mawson, 1939

Type species: *Pot. finlaysoni* Johnston & Mawson, 1939.
Other species: *Pot. aepyprymnus* Mawson, 1974; *Pot. temperatus* Smales, 1997; *Pot. tropicus* Smales, 1997; *Pot. woyliei* Smales, 2005.

Generic definition: cephalic collar present; cervical cuticle inflated; 6 lips present; sub-medial papillae and amphids borne on lips with 2 interlabia in dorsal and ventral positions; buccal capsule shallow, wider than long, without transverse striations; oesophagus with distinct corpus, isthmus and bulb; bulb lined with 3 pairs of sclerotised plates; nerve ring in anterior oesophageal region; deirid and excretory pore immediately posterior to nerve ring; gubernaculum absent; ovejector J-shaped.

Key to species of Potorostrongylus

1a. Buccal capsule extends beyond cervical collar (Fig. 34 D) . . . *Pot. aepyprymnus*
1b. Buccal capsule does not extend beyond cervical collar 2

2a. Spicules < 1.0 mm; vagina < 0.23 mm . *Pot. woyliei*
2b. Spicules > 1.0 mm; vagina >0.23 mm. 3

3a. Dorsal lobe of bursa elongate (Fig. 34 G); vulva to posterior end > 0.6mm. 4
3b. Dorsal lobe of bursa no longer than lateral lobes (Fig. 34 I); vulva to posterior end < 0.6 mm . . . . . *Pot. temperatus*

4a. Deirids stout, posterior to excretory pore (Fig. 34 A); spicule tips straight; vagina 0.34–0.54 mm . . . . . *Pot. finlaysoni*
4b. Deirids fine, at level of excretory pore; spicule tips curved; vagina 0.50–0.64 mm . . . . . *Pot. tropicus*

Potorostrongylus aepyprymnus Mawson, 1974

Potorostrongylus aepyprymnus Mawson, 1974, p. 137, figs 7–12; Smales, 1997c, pp. 189–190, figs 16–24.
Type data: holotype SAM V1692, allotype SAM V1693, paratypes SAM AHC 5811.
Type locality: Warwick, Qld (28° 13'S 152° 02'E).
Type host: *Aepyprymnus rufescens* (Gray, 1837).
Site in host: stomach.
Distribution: south-eastern Qld.
Diagnostic features (Figs 34 D, E): Males 5.0–8.0 mm; females 5.0–5.5 mm; buccal capsule extends posterior to level of cephalic collar; dorsal lobe of bursa no longer than lateral lobes; spicules 0.96–1.05 mm; ala terminates anterior to tip; female tail 0.54–0.68 mm; ovejector J-shaped.

Potorostrongylus finlaysoni Johnston & Mawson, 1939

Potorostrongylus finlaysoni Johnston & Mawson, 1939d, pp. 308–309, figs 1–4; Skrjabin et al, 1952, p. 296; Popova, 1960, p. 220; Munday & Green, 1972, p. 7; Mawson, 1974, pp. 135–137, figs 1–6; Smales, 1997c, pp. 186–189, figs 1–15; 2005, p. 29.
Zoniolaimus (*Potorostrongylus*) *finlaysoni*: Yamaguti, p. 404.

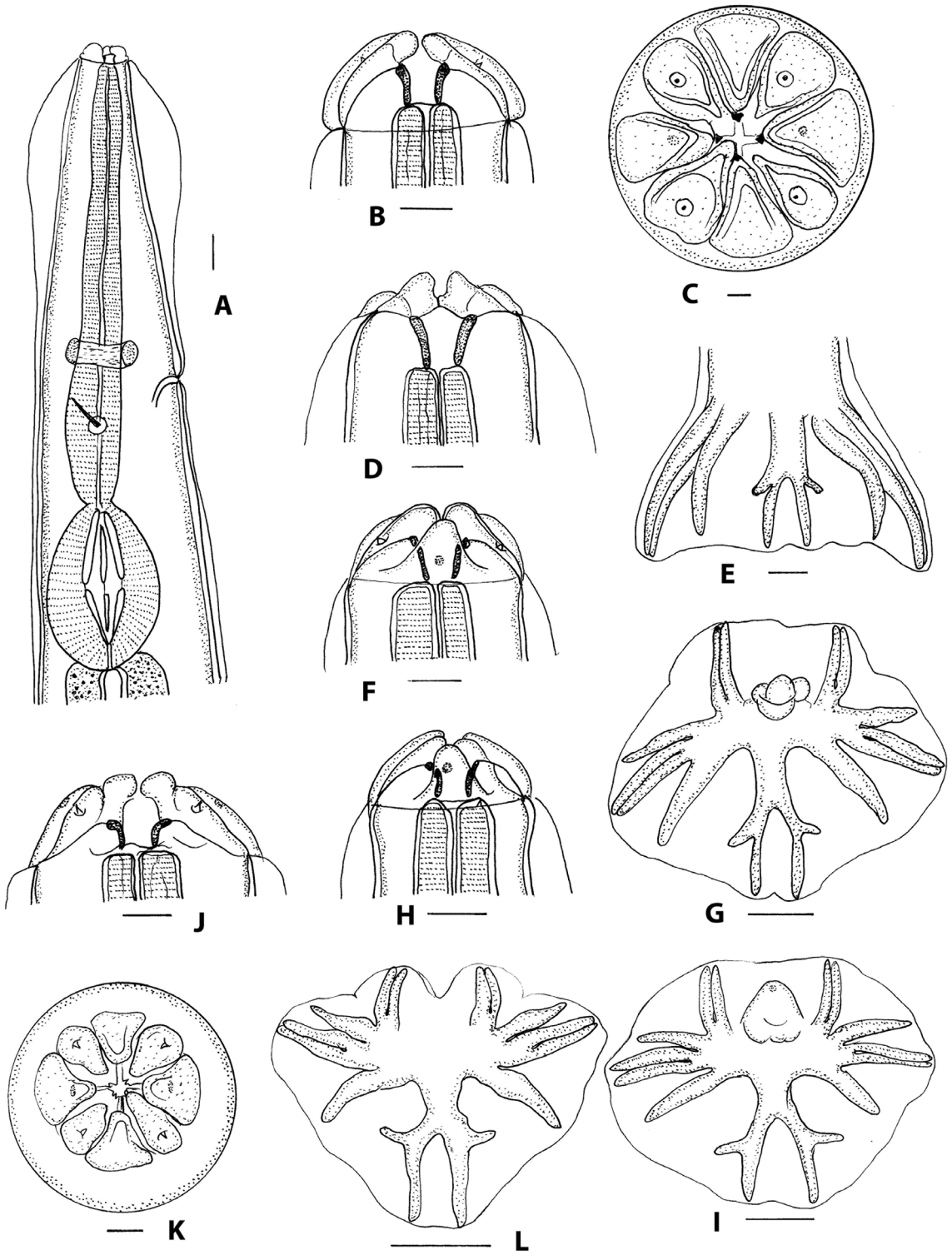


Fig. 34. Genus *Potorostrongylus*. A, *Potorostrongylus finlaysoni*, oesophagus, lateral view; B, *Pot. finlaysoni*, buccal capsule, lateral view; C, *Pot. finlaysoni*, mouth opening, apical view; D, *Potorostrongylus aepyprymnus*, buccal capsule, lateral view; E, *Pot. aepyprymnus*, bursa, dorsal view; F, *Potorostrongylus tropicus*, buccal capsule, lateral view; G, *Pot. tropicus*, bursa, apical view; H, *Potorostrongylus temperatus*, buccal capsule, lateral view; I, *Pot. temperatus*, bursa, apical view; J, *Potorostrongylus woyliei*, buccal capsule, lateral view; K, *Pot. woyliei*, mouth opening, apical view; L, *Pot. woyliei*, bursa, apical view. (A, C, from Mawson, 1974; B, D–I from Smales, 1997c; J–L, from Smales, 2005).

Scale-bars: A, L, 0.1 mm; B, D–I, J, K, 0.025 mm; C, 0.01 mm.

Type data: holotype and allotype SAM V1378, paratypes SAM AHC 30449.
Type locality: Cape Conran, Vic. (37° 49′S 148° 44′E).
Type host: *Potorous tridactylus* (Kerr,1792).
Other hosts: *Bettongia gaimardi* (Desmarest).
Location in host: stomach.
Distribution: Tas, Vic, south-eastern Qld.
Representative DNA sequence data: ITS1, 2: FR854224.
Diagnostic features (Figs 34 A–C): Males 6.0–11.0 mm; females 6.0–13.0 mm; buccal capsule does not extend posterior to level of cephalic collar; dorsal lobe of bursa longer than lateral lobes; spicules 1.22–1.64 mm; ala diminishes gradually to tip; female tail 0.60–1.11 mm; ovejector J-shaped.

***Potorostrongylus temperatus* Smales, 1997**

Potorostrongylus temperatus Smales, 1997c, pp. 193–195, figs 37–50; Smales, 2005, p. 28.
Type data: holotype SAM AHC 30453, allotype SAM AHC 30454, paratypes SAM AHC 9989.
Type locality: Launceston, Tas (41° 27′S 147° 10′E).
Type host: *Bettongia gaimardi* (Desmarest, 1822).
Other hosts: *Aepyprymnus rufescens* (Gray, 1837).
Site in host: stomach.
Distribution: Tas, north-eastern NSW.
Diagnostic features: Males 8.0–12.0 mm; females 9.0–12.0 mm; buccal capsule does not extend posterior to level of cephalic collar; dorsal lobe of bursa no longer than lateral lobes; spicules 1.10–1.30 mm; ala diminished gradually to tip; female tail 0.67–0.83 mm; ovejector J-shaped.

***Potorostrongylus tropicus* Smales, 1997**

Potorostrongylus tropicus Smales, 1997c, pp. 191–193, figs 25–36; 2005, p. 28.
Type data: holotype SAM AHC 30452, allotype SAM AHC 30452, paratypes SAM AHC 7163, 11102.
Type locality: Davies Creek National Park, Qld (17° 01′S 145° 30′E).
Type host: *Bettongia tropica* Wakefield, 1967.
Site in host: stomach.
Distribution: north-eastern Qld.
Representative DNA sequence data: ITS1, 2: FR854223.
Diagnostic features (Figs 34 F, G): Males 9.0–11.0 mm; females 9.0–12.0 mm; buccal capsule extends posterior to level of cephalic collar; dorsal lobe of bursa longer than lateral lobes; spicules 1.16–1.35 mm; ala diminishes gradually to tip; female tail 0.54–0.68 mm; ovejector J-shaped.

***Potorostrongylus woyliei* Smales, 2005**

Potorostrongylus woyliei Smales, 2005, p. 29, figs 1–17.
Type data: holotype SAM AHC 32862, allotype SAM AHC 32863, paratypes SAM AHC 32864.
Type locality: Batalling, WA (33° 20′S 116° 34′E).
Type host: *Bettongia penicillata* Gray, 1837.
Site in host: stomach.
Distribution: south-western WA.
Diagnostic features (Figs 34 J–L): Males 8.6–10.0 mm; females 11.0–12.0 mm; buccal capsule does not extend posterior to level of cephalic collar; dorsal lobe of bursa longer than lateral lobes; spicules 0.68–0.99 mm; ala diminished gradually to tip; female tail 0.60–0.75 mm; ovejector J-shaped.

Rugopharynx Mönnig, 1927

Syn: *Rugonema* Beveridge, 1989.

Type species: *R. australis* (Mönnig, 1926).
Other species: *R. alpha* (Johnston & Mawson, 1938); *R. chi* Beveridge & Chilton, 1999; *R. delta* (Johnston & Mawson, 1939); *R. disiunctus* Beveridge, 2020; *R. epsilon* (Johnston & Mawson, 1939); *R. labiatus* (Beveridge, 1999); *R. longibursaris* (Kung, 1948); *R. longispicularis* Beveridge & Chilton, 1999; *R. macropodis* Beveridge & Chilton, 1999; *R. mawsonae* Beveridge, Chilton & Andrews, 1994; *R. moennigi* Beveridge, Sukee & Jabar, 2021; *R. mu* Beveridge & Chilton, 1999; *R. omega* Beveridge, 1982; *R. petrogale* Beveridge & Chilton, 1999; *R. pi* Beveridge & Chilton, 1999; *R. rho* Beveridge & Chilton, 1999; *R. rosemariae* Beveridge & Presidente, 1978; *R. rufogriseus* Magzoub, 1964; *R. sigma* Chilton, Beveridge & Andrews, 1992; *R. setonicis* Appan, Bergfield & Beveridge, 2004; *R. solitarius* Beveridge, 2020; *R. spratti* Beveridge & Chilton, 1999; *R. tau* Beveridge & Chilton, 1999; *R. theta* (Johnston & Mawson, 1939); *R. thetidis* Beveridge, 2020; *R. thylogale* Beveridge, 2020; *R. zeta* (Johnston & Mawson, 1939).

Generic definition: Cephalic collar present; labial collar present internal to cephalic collar; cephalic papillae conical, with single or paired setae; mouth opening circular (dorso–ventrally elongate in *R. rosemariae*); leaf crown absent; buccal capsule longer than wide, heavily sclerotized, with prominent or faint transverse striations; oesophageal corpus short with isthmus and pyriform bulb; nerve ring at level

of isthmus or in anterior oesophageal region; excretory pore at level of nerve ring or in anterior oesophageal region; deirid at level of buccal capsule or in anterior oesophageal region; bursa with sclerotized bosses (except *R. theta*); spicules elongate, alate; ovejector J-shaped.

Comments: The complexity of this genus has gradually been revealed by allozyme and sequence data (Beveridge et al., 1994, Chilton et al., 1993, 1996, 2016c). Many species are identifiable based on the features and surface structure of the buccal capsule (Fig. 36), but additional features such as the position of the nerve ring, the bursa, and the morphology of the spicule tips are of importance in the *R. australis* and *R. zeta* species complexes (Fig. 35).

Key to species of Rugopharynx

(Due to intra–specific variation, some species are included in the key more than once).

1a. Buccal capsule prominently trilobed (Figs 36 J, L) 3
1b. Buccal capsule not prominently trilobed 2

2a. Buccal capsule subdivided into 2 equal lobes (Fig. 36 D) . . . . . *R. epsilon*
2b. Buccal capsule with either unequal lobes or without lobes 12

3a. Spicules > 1.25 mm 4
3b. Spicules < 1.25 mm 6

4a. Deirids immediately post-buccal; externo-dorsal ray stout; external branchlets of dorsal ray arising at bifurcation . . . . . *R. mawsonae*
4b. Deirids in anterior oesophageal region; externo-dorsal ray slender; external branchlets of dorsal ray arising after bifurcation. 5

5a. Spicule ala diminishes gradually towards tip (Fig. 35 O); spicules 1.72–2.15 mm; elevations of cuticle containing external branchlets of dorsal ray extending to margin of bursa (Fig. 35 G) . . . . . *R. solitarius*
5b. Spicule ala terminates abruptly at spicule tip; spicules 1.57–1.75 mm; elevations of cuticle containing external branchlets of dorsal ray locally circumscribed . . . . . *R. zeta*

6a. Spicules < 0.65 mm; external branchlets of dorsal ray arising anterior to major bifurcation . . . . . *R. delta*
6b. Spicules > 0.65 mm; external branchlets of dorsal ray arising at or posterior to major bifurcation. . 7

7a. Spicule tips prominently sinuous (Fig. 35 L) . . . . . *R. thetidis*
7b. Spicule tips not prominently sinuous 8

8a. Dorsal lobe of bursa extremely elongated; internal branchlets twice as long as common trunk (Fig. 35 H) . . . . . *R. thylogale*
8b. Dorsal lobe of bursa not extremely elongated; internal branchlets at most 1.5 times as long as common trunk. 9

9a. Nerve ring in anterior oesophageal region . . . . . *R. petrogale*
9b. Nerve ring at anterior extremity of oesophageal isthmus 10

10a. Deirid immediately post-buccal. . . . . *R. sigma*
10b. Deirid in anterior oesophageal region 11

11a. Spicules 0.82–1.04 mm; spicule ala terminates in complex whorls around spicule tip (Fig. 35 J) . . . . . *R. longibursaris*
11b. Spicules 0.65–0.83 mm; spicule ala terminates in sharp point (Fig. 35 N) . . *R. omega*

12a. Oesophagus lined with prominent sclerotized bosses; spicules > 3.5 mm . . . . . *R. rosemariae*
12b. Oesophageal lining without prominent sclerotized bosses; spicules < 3.0 mm 13

13a. Nerve ring in anterior oesophageal region (Fig. 35 B) 14
13b. Nerve ring surrounds oesophageal isthmus (Fig. 35 A) 17

14a. Spicules < 1.4 mm 15
14b. Spicules > 1.5 mm 16

15a. Spicules 0.89–1.05 mm; external branchlets of dorsal ray arise after principal bifurcation . . . . . *R. petrogale*
15b. Spicules 1.00–1.34 mm; external branchlets of dorsal ray arise at principal bifurcation . . . . . *R. setonicis*

16a. Spicules 1.65–1.96 mm; external branchlets of dorsal ray arise at principal bifurcation . . . . . *R. rho*
16b. Spicules 1.95–2.33 mm; external branchlets of dorsal ray arise after principal bifurcation . . . . . *R. disjunctus*

17a. Bursa without sclerotized bosses . . . . *R. theta*
17b. Bursa with sclerotized bosses 18

18a. Bursa with very large bosses (Fig. 35 E); female tail truncated (Fig. 35 D) . . *R. rufogriseus*
18b. Bursa with fine sclerotized bosses; female tail conical 19

19a. Spicules 2.41–2.65 mm . . . . *R. longispicularis*
19b. Spicules < 2.2 mm 20

20a. Buccal capsule much longer than wide, > twice as long as wide (Fig. 36 C) 21
20b. Buccal capsule slightly longer than wide; length: width ratio < 1.7 (Fig. 36 G) 23

21a. Cephalic collar projects into mouth opening with 4 lip–like projections in dorsal, ventral and lateral positions (Fig. 36 I) . . . . *R. labiatus*
21b. Cephalic collar without lip-like projections at mouth opening 22

22a. Oesophagus 0.80–0.89 mm in male, 0.74–0.94 mm in female; parasitic in *Mac. fuliginosus* or *Mac. giganteus* . . . *R. macropodis*
22b. Oesophagus 0.52–0.75 mm in male, 0.57–0.86 mm in female; parasitic in *N. rufogriseus* (or *N. parryi*) . . . . . *.R. pi*

23a. Dorsal lobe of bursa longer than lateral lobes; buccal capsule prominently lobed at anterior extremity (Figs 36 G, H) 24
23b. Dorsal lobe of bursa as long as lateral lobes; buccal capsule not prominently lobed at anterior extremity (Figs 36 A, F) 26

24a. Buccal capsule striations extremely prominent; female tail 0.40–0.48 mm . . *R. spratti*
24b. Buccal capsule striations faint; female tail 0.24–0.37 mm 25

25a. Spicules >1.2 mm ; gubernaculum absent . *R. tau*
25b. Spicules < 1.2 mm ; gubernaculum present . *R. chi*

26a. Transverse striations of buccal capsule regular, uniform (Fig. 36 F) . . . . . *R. mu*
26b. Striations on parts of buccal capsule irregular, interrupted, not forming regular transverse lines (Fig. 36 A) 27

27a. Buccal capsule mildly three-lobed (Fig. 36 K) . . . . . *.R. zeta*
27b. Buccal capsule not three-lobed. 28

28a. Buccal capsule length: width ratio 1.65; spicule ala terminates anterior to spicule tip . . . . . *R. alpha*
28b. Buccal capsule length: width ratio 1.50; spicule ala diminishes to spicule tip 29

29a. Spicules 1.60–2.15 mm . . . . . *R. australis**
29b. Spicule length 1.13–1.68 mm . . . *R. moennigi**
* sibling species, potentially difficult to identify

***Rugopharynx alpha* (Johnston & Mawson, 1938)**

Pharyngostrongylus alpha Johnston & Mawson, 1938, pp. 264–266, figs 1–5.
Rugopharynx alpha: Yamaguti, 1961, p. 409; Beveridge & Chilton, 1999, pp. 836–839, figs 100–105; Bradley et al., 2000, p. 39.
Pharyngostrongylus beta Johnston & Mawson, 1938, pp. 264, 266, figs 6–8.
Rugopharynx beta: Yamaguti, 1961, p. 409.
Rugopharynx australis (in part): Beveridge, 1982, p. 74; Beveridge et al., 1989, p. 277.
Type data: holotype and allotype SAM V1365; holotype and allotype of *R. beta*, SAM V1366.
Type locality: Mount Liebig, NT (23° 17'S 131° 21'E).
Type host: *Petrogale lateralis* Gould, 1840 (MacDonnell Ranges race).
Other hosts: *Petrogale purpureicollis* Le Souef, 1924.
Site in host: stomach.
Distribution: NT (Central Australia); north-western Qld. Map: Beveridge & Chilton, 1999, p. 837.
Representative DNA sequence data: ITS1, 2: LN906946.
Diagnostic features: Males 3.9–5.7 mm; females 5.0–6.7 mm; buccal capsule short, anterior extremity slightly widened; transverse striations irregular, interrupted; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; spicules 1.35–1.64 mm; spicule ala terminates gradually anterior to spicule tip; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.
Comments: *Rugopharynx alpha* has often been treated

as a synonym of *R. australis*, but was resurrected by Beveridge & Chilton (1999) based on differences in spicule lengths, the morphology of the spicule ala and the dorsal lobe of the bursa. The validity of the species is supported by DNA sequence data (Chilton et al., 2016c).

***Rugopharynx australis* (Mönnig, 1926)**

Spirostrongylus australis Mönnig, 1926, pp. 263–265, figs 4–9.

Rugopharynx australis: Mönnig, 1927, p. 265; Wood, 1929b, pp. 552–554; Yamaguti, 1961, p. 409; Mawson, 1964, pp. 245–248, figs 32–39; Mykytowycz, 1964, p. 682; Wahid, 1964, pp. 186, 188–189, figs 12–17; Arundel et al., 1979, pp. 365, 370; Beveridge & Arundel, 1979, p. 72; Beveridge, 1982, pp. 75–78, figs 258–271; Beveridge & Chilton, 1999, pp. 807–812, figs 1–16; Beveridge et al. 1989, p. 277; Pamment et al., 1994, p. 191; Hoste & Beveridge, 1993, p. 172; Chilton et al., 1996, p. 129; Turni & Smales, 2001, p. 406; Spratt & Beveridge, 2016, p. 125; Beveridge, 2020c, p. 4, 2020d, p. 270; 2020e, p. 204; Beveridge et al., 2021, p. 681.

Pharyngostrongylus australis: Wood, 1931, p. 554; Popova, 1958, pp. 238–241, fig. 161.

Pharyngostrongylus brevis Cavanan, 1931, pp. 199–201, figs 1–5.

Type data: syntypes in OVRI T2017, SAM AHC 2468.

Type locality: National Zoological Gardens, Pretoria, South Africa.

Type host: *Osphranter rufus* (Desmarest, 1822).

Other hosts: *Dendrolagus matschiei* Forster & Rothschild, 1907 (captive host); *Macropus fuliginosus* (Desmarest, 1817); *Macropus giganteus* Shaw, 1790; *Notamacropus agilis* (Gould, 1842) (captive host); *Notamacropus dorsalis* (Gray, 1837); *Onychogalea fraenata* (Gould, 1840); *Osphranter bernardus* (Rothschild, 1904) (captive host); *Osphranter robustus* (Gould, 1840); *Petrogale xanthopus* Gray, 1855.

Site in host: stomach.

Distribution: inland areas of NT, Qld, NSW, Vic, WA. Maps: Beveridge & Chilton, 1999, p. 812; Beveridge, 2020d, p. 270; Beveridge et al., 2021, p. 684.

Representative DNA sequence data: ITS1, 2: LN906948–53.

Diagnostic features (Figs 35 A, 36 A): Males 6.7–10.5 mm; females 6.8–10.1 mm; buccal capsule short, anterior extremity slightly widened; transverse striations irregular, interrupted; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa as long as or longer than lateral lobes; spicules 1.60–2.15 mm; spicule ala diminishes gradually towards tip; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.

Comments: *Rugopharynx australis* was recognised as a morphologically polymorphic species by Beveridge (1982). Subsequent electrophoretic studies (Chilton et al., 1996) confirmed that populations of nematodes in certain host species were genetically distinct leading to the erection of nine new species formerly included under this name (Beveridge & Chilton, 1999). Subsequent DNA sequence data (Chilton et al., 2016c) provided support for the erection of the new species. However, it also indicated that, based on both morphological (Beveridge & Chilton, 1999) and molecular evidence (Chilton et al., 2016c), *R. australis* as re-defined by Beveridge & Chilton (1999) still consisted of two related species, sometimes occurring in the same host individual. Subsequent studies have led to the separation of *R. moennigi* from *R. australis*, but mixed infections are common and the two species can be difficult to separate (Beveridge et al., 2021). Consequently, some of the citations for *R. australis* may not refer exclusively to this species.

***Rugopharynx chi* Beveridge & Chilton, 1999**

Rugopharynx chi Beveridge & Chilton, 1999, pp. 830–832, figs 75–83.

Rugopharynx australis (in part): Munday & Green, 1972, p.7.

Type data: holotype and allotype, SAM AHC 31229, paratypes SAM AHC 31230.

Type locality: Launceston, Tas. (41° 27′S 147° 10′E).

Type host: *Thylogale billardierii* (Desmarest, 1822).

Site in host: stomach.

Distribution: Tas. Map: Beveridge & Chilton, 1999, p. 833.

Representative DNA sequence data: ITS1, 2: LN906954.

Diagnostic features (Fig. 36 G): Males 4.0–6.1 mm; females 4.9–6.8mm; buccal capsule short, very slightly bilobed; transverse striations regular, faint; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; spicules 0.69–1.20 mm; spicule ala terminates abruptly anterior to tip; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.

***Rugopharynx delta* (Johnston & Mawson, 1939)**

Pharyngostrongylus delta Johnston & Mawson, 1939a, p. 136, figs 40–43; 1939b, p. 517; 1939d, p. 307; Popova, 1958, p. 243.

Rugopharynx delta: Yamaguti, 1961, p. 409; Wahid, 1964, p. 186; Mawson, 1965, pp. 155, 157, figs 43–47; Kidd & Evans, 1972, pp. 480–481; Beveridge, 1982, pp. 63–65, figs 221–229; Beveridge et al., 1995, p. 152; 1998, p. 482.
Type data: holotype and allotype SAM V1553.
Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).
Type host: *Notamacropus dorsalis* (Gray, 1837).
Other hosts: other published host records: *Macropus giganteus* Shaw, 1790, *Notamacropus rufogriseus* Desmarest, 1817, *Osphranter rufus* (Desmarest, 1822) (captive), *Thylogale thetis* (Lesson, 1827) and *T. billardierii* (Desmarest, 1822) have not been confirmed (Beveridge, 1982).
Site in host: stomach.
Distribution: eastern Qld.
Representative DNA sequence data: ITS1, 2: LN906955.
Diagnostic features: Males 3.3–5.1 mm; females 3.9–6.2 mm; buccal capsule prominently trilobed; deirid in anterior oesophageal region; spicules 0.55–0.64 mm; lateral branchlets of dorsal ray arising prior to principal bifurcation; ovejector J-shaped.
Comments: Although a variety of host species has been reported in the literature, recent collections have identified only *N. dorsalis* as a host of this species (Beveridge, 1982; Beveridge et al., 1998). The additional published host records for this nematode species remain to be confirmed.

***Rugopharynx disiunctus* Beveridge, 2020**

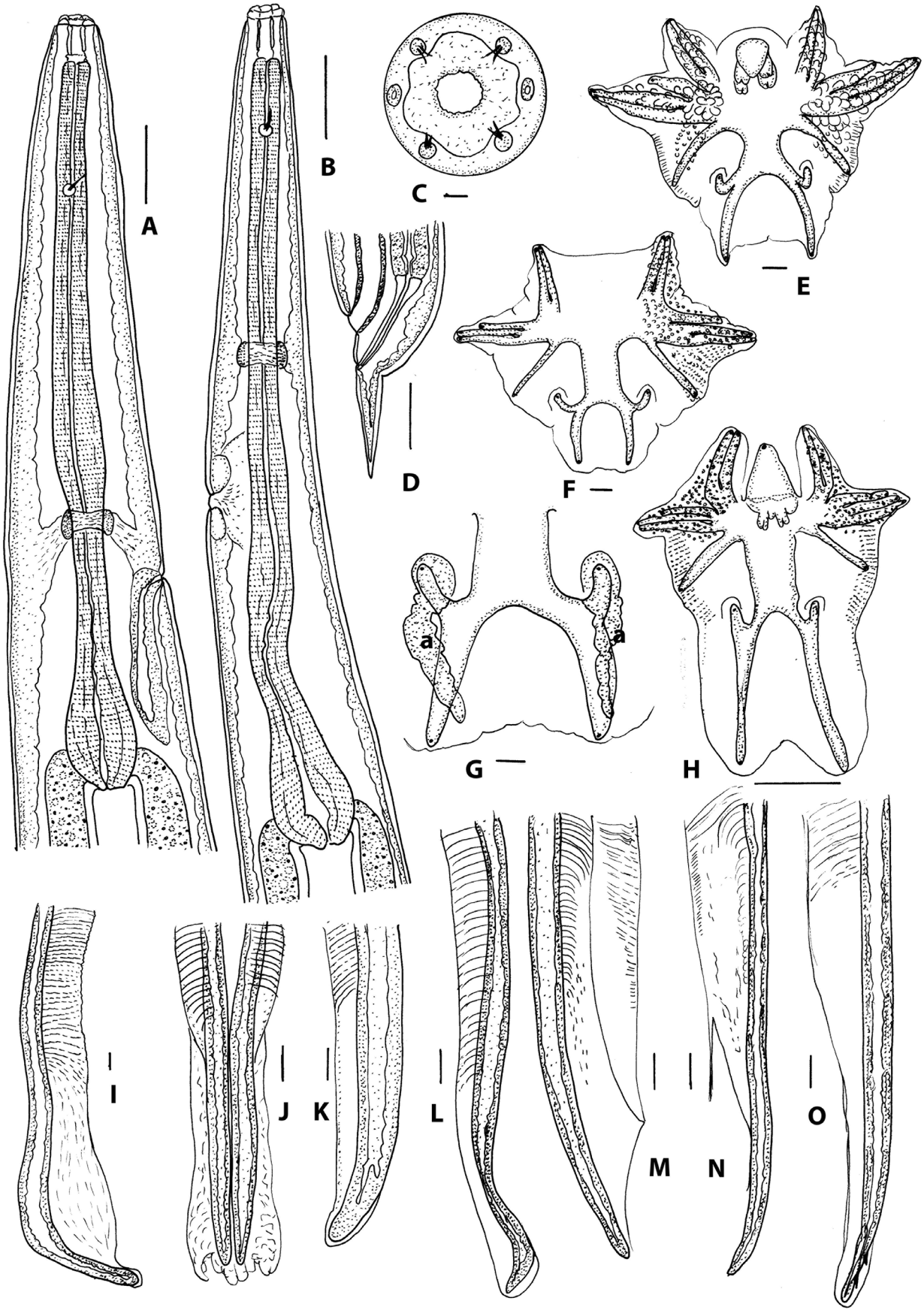
Rugopharynx disiunctus Beveridge, 2020a, pp. 51–53, figs 36–46.
Type data: holotype SAM AHC 48781, allotype SAM AHC 48782, paratypes SAM AHC 31893, BMNH 2019.8.12.7–16.
Type locality: Waroona, WA (32° 52′S 115° 55′E).
Type host: *Macropus fuliginosus* (Desmarest, 1817).
Other hosts: *Notamacropus irma* (Jourdan, 1837).
Site in host: stomach.
Distribution: south-western WA; southern SA. Map: Beveridge, 2020a, p. 53.
Representative DNA sequence data: ITS1, 2: LN906978.
Diagnostic features: Males 6.9–8.4 mm; females 7.7–8.9 mm; buccal capsule long; transverse striations regular, faint; nerve ring in anterior oesophageal region; deirid post-buccal; dorsal lobe of bursa slightly longer than lateral lobes; spicules 1.95–2.33 mm; spicule ala terminates at tip; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.
Comments: This species was formerly included within *R. rho* by Beveridge & Chilton (1999).

***Rugopharynx epsilon* (Johnston & Mawson, 1939)**

Pharyngostrongylus epsilon Johnston & Mawson, 1939a, pp. 137–138, figs 44–46; 1939b, pp. 513, 517; 1939d, p. 307; Popova, 1958, pp. 243–244.
Rugopharynx epsilon: Yamaguti, 1961, p. 409; Wahid, 1964, p. 188; Mawson, 1965, pp. 154–155, figs 37–70; Munday & Green, 1972, p. 7; Beveridge, 1982, pp. 55–58, figs 183–190; Beveridge et al., 1985, p. 378; 1998, p. 482; Aussavy et al., 2011, pp. 16, 17; Vendl & Beveridge, 2014, pp. 108, 109; Beveridge, 2016, p. 211; Spratt et al., 2017, pp. 241, 242.
Type data: holotype SAM V1554.
Type locality: Eidsvold, Qld (25° 22′S 151° 07′E).
Type host: *Notamacropus dorsalis* (Gray, 1837).
Other hosts: *Notamacropus parma* (Waterhouse, 1846); *Notamacropus parryi* (Bennett, 1835); *Notamacropus rufogriseus* (Desmarest, 1817); *Wallabia bicolor* (Desmarest, 1804). Unconfirmed records from: *Thylogale billardierii* (Desmarest, 1822); *Thylogale stigmatica* (Gould, 1860); *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: Qld, NSW, Vic, Tas.
Representative DNA sequence data: ITS1, 2: LN906956–60.
Diagnostic features (Figs 36 D, 45 E): Males 6.2–6.9 mm; females 7.0–8.1 mm; buccal capsule prominently bilobed; lobes equal; nerve ring encircles oesophageal

Fig. 35. Genus *Rugopharynx*. A, *Rugopharynx australis*, oesophagus, lateral view; B, *Rugopharynx rho*, oesophagus, lateral view; C, *Rugopharynx zeta*, anterior end, apical view; D, *Rugopharynx rufogriseus*, female tail, lateral view; E, *R. rufogriseus*, bursa, apical view; F, *Rugopharynx mu*, bursa, apical view; G, *Rugopharynx solitarius*; dorsal lobe of bursa, dorsal view; H, *Rugopharynx thylogale*, bursa, apical view; I, *Rugopharynx longispicularis*, spicule tip, lateral view; J, *R. longibursaris*, spicule tips, dorso-ventral view; K, *Rugopharynx mawsonae*, spicule tip, lateral view; L, *Rugopharynx thetidis*, spicule tip, lateral view; M, *Rugopharynx sigma*, spicule tip, lateral view; N, *Rugopharynx omega*, spicule tip, lateral view; O, *Rugopharynx solitarius*, spicule tip, lateral view. (A, B, F, I, from Beveridge & Chilton, 1999; C, K, from Beveridge et al., 1994; D, E, J, from Beveridge, 1982; G, H, L, O, from Beveridge, 2020a; M, N from Chilton et al., 1993).

Scale-bars: A, B, D, H, 0.1 mm; C, E–G, I–O, 0.01 mm.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isthmus; deirid in mid-oesophageal region; spicules 1.02–1.26 mm; lateral branchlets of dorsal ray arising after principal bifurcation; spicule ala diminishes gradually towards tip; ovejector J-shaped.

Comments: *Rugopharynx epsilon* has been reported from a wide range of hosts, but the records from *Thylogale* spp. have not been confirmed (Beveridge et al., 1992; Griffith et al., 2000) and there are no specimens in museum collections to support the records. The record from *Thyl. thetis* from New England, NSW, appears to have been a misidentification of *N. dorsalis* (see Beveridge, 1982, p. 81). Sequence data have confirmed the conspecificity of representatives of this species from *N. rufogriseus* and *Wal. bicolor* (Chilton et al., 2016c).

***Rugopharynx labiatus* (Beveridge, 1999)**

Rugonema labiatum Beveridge, 1999a, pp. 230–232, figs 1–12.

Rugopharynx labiatus: Chilton et al., 2016c, p. 126 (as *labiatum*).

Type data: holotype SAM AHC 31186, allotype SAM AHC 31187, paratypes SAM AHC 7366.

Type locality: Perth, WA (31° 57′S 115° 52′E).

Type host: *Notamacropus irma* (Jourdan, 1837).

Site in host: stomach.

Distribution: south-western WA.

Representative DNA sequence data: ITS1, 2: LN906995.

Diagnostic features (Fig. 36 I): Males 4.7–5.7 mm; females 4.7–6.1 mm; labial collar forming 4 small lips in lateral, dorsal and ventral positions; buccal capsule long; transverse striations regular, prominent; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa no longer than lateral lobes; spicules 1.24–1.37 mm; spicule ala terminates at tip, enlarged distally; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.

Comments: Beveridge (1999) placed this species in an independent genus, but in the molecular analysis of Chilton et al. (2016c), it nested within species of *Rugopharynx*. *Rugonema* is therefore treated here as a synonym of *Rugopharynx* and as this name is masculine, the specific epithet has been altered accordingly.

***Rugopharynx longibursaris* (Kung, 1948)**

Pharyngostrongylus longibursaris Kung, 1948, pp. 97–100, figs. 6–12; Popova, 1958, pp. 246–247, fig. 166 (as *P. longibursatus*);

Rugopharynx longibursaris: Yamaguti, 1961, p. 410; Wahid, 1964, p. 188; Mawson, 1965, p. 155 (as *R. zeta*); Beveridge, 1982, pp. 66–69, figs 230–238; Chilton et al., 1993, p. 159; Beveridge et al., 1995, p. 152; Aussavy et al., 2011, pp. 16; Schultz et al., 2011, p. 239; Vendl & Beveridge, 2014, p.108.

Type data: syntypes BMNH 1949.12.23.26–55.

Type locality: London Zoological Gardens.

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Other hosts: *Petrogale penicillata* (Gray,1827).

Site in host: stomach.

Distribution: western Vic, south-eastern SA, Tas. Map: Chilton et al., 1993, p. 162.

Representative DNA sequence data: ITS1, 2: LN906961–2.

Diagnostic features (Fig. 35 R): Males 4.4–7.0 mm; females 5.9–6.6 mm; buccal capsule prominently trilobed; deirid in anterior oesophageal region; nerve ring encircles oesophageal isthmus; dorsal lobe of bursa longer than lateral lobes; spicules 0.82–1.04 mm; lateral branchlets of dorsal ray arising after principal bifurcation; ala of spicule tip forming elaborate expansion surrounding spicule tips; ovejector J-shaped.

Comments: This species is found only in Tasmania, the west of Victoria and the adjacent south-east of South Australia. Along the east coast, it is replaced by *R. omega*. The single record from *Pet. penicillata* (Schultz et al., 2011) is from a captive-bred animal released into a zone of sympatry with *N. rufogriseus* in western Victoria.

***Rugopharynx longispicularis* Beveridge & Chilton, 1999**

Rugopharynx longispicularis Beveridge & Chilton, 1999, pp. 823–824, figs 48–55.

Type data: holotype SAM AHC 31223, allotype SAM AHC 31224, paratypes SAM AHC 31225.

Type locality: Taree, NSW (31° 54′S 152° 27′E).

Type host: *Notamacropus parma* (Waterhouse, 1846).

Other hosts: *Notamacropus parryi* (Bennett, 1835) (captive host).

Site in host: stomach.

Distribution: eastern NSW.

Diagnostic features (Fig. 35 R): Males 5.0–5.4 mm; females 5.9–6.3 mm; buccal capsule short; transverse striations regular, prominent; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa no longer than lateral lobes; spicules 2.41–2.65 mm; spicule prominently recurved near tip, ala terminates abruptly anterior to tip, enlarged distally; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.

***Rugopharynx macropodis* Beveridge & Chilton, 1999**

Rugopharynx macropodis Beveridge & Chilton, 1999, pp. 812–817, figs 17–28; Webley et al., 2004, p. 625; Aussavy et al., 2011, pp. 14, 15; Cripps et al., 2015, p. 168; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 240; Beveridge, 2020d, p. 270.

Type data: holotype SAM AHC 31215, allotype SAM AHC 31216, paratypes SAM AHC 31217, BMNH 1998.6.3.22–23.

Type locality: Avalon, Vic (38° 05′S 144° 26′E).

Type host: *Macropus giganteus* Shaw, 1790.

Other hosts: *Macropus fuliginosus* (Desmarest, 1817).

Site in host: stomach.

Distribution: southern SA, Vic, Tas, eastern NSW, south-eastern Qld, south-western WA. Maps: Beveridge & Chilton, 1999, p. 816; Beveridge 2020d, p. 270.

Representative DNA sequence data: ITS1, 2: LN906963–5.

Diagnostic features (Fig. 36 C): Males 6.2–6.8 mm; females 7.1–8.5 mm; buccal capsule long; transverse striations regular, prominent; nerve ring encircles oesophageal isthmus; deirid post-buccal; dorsal lobe of bursa no longer than lateral lobes; spicules 0.08–1.25 mm; spicule ala terminates at tip; external branchlets of dorsal ray arising immediately after principal bifurcation; ovejector J-shaped.

Comments: Prior to 1999, this species was confused with *R. australis*. It occurs generally in higher rainfall regions in the south of the continent, but can occur in mixed infections with *R. australis* in some inland areas (Beveridge & Chilton, 1999).

***Rugopharynx mawsonae* Beveridge, Chilton & Andrews, 1994**

Rugopharynx mawsonae Beveridge, Chilton & Andrews, 1994, pp. 165–168, figs 13–20; Beveridge et al., 1995, p. 152; Beveridge et al., 1998, p. 482.

Type data: holotype SAM AHC 22846, allotype SAM AHC 22847, paratypes SAM AHC 12275, 22853.

Type locality: Apis Creek Station via Marlborough, Qld (22° 59′S 149° 34′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Site in host: stomach.

Distribution: eastern Qld. Map: Beveridge et al., 1994, p. 21.

Representative DNA sequence data: ITS1, 2: LN906966–8.

Diagnostic features (Figs 35 K, 36 L): Males 6.1–7.8 mm; females 6.3–8.7 mm; buccal capsule prominently trilobed; nerve ring encircles oesophageal isthmus; deirid immediately post-buccal; spicules 1.28–1.48 mm; dorsal lobe of bursa as long as lateral lobes; externo-dorsal ray stout; lateral branchlets of dorsal ray arising at principal bifurcation; spicule ala diminishing gradually in width towards tip; ovejector J-shaped.

***Rugopharynx moennigi* Beveridge, Sukee & Jabbar, 2021**

Rugopharynx moennigi Beveridge, Sukee & Jabbar, 2021, p. 687, fig. 5.

Type data: holotype SAM AHC 49098, allotype SAM AHC 49099, paratypes SAM AHC 30916.

Type locality: Hattah-Kulkyne National Park, Vic. (8° 34′S 142° 20′E).

Type host: *Macropus fuliginosus* (Desmarest, 1817).

Other hosts: *Macropus giganteus* Shaw, 1790; *Osphranter robustus* (Gould, 1840); *Osphranter rufus* (Desmarest, 1822).

Site in host: stomach.

Distribution: southern Qld, NSW, Vic, SA, southern WA. Map: Beveridge et al., 2021, p. 688.

Representative DNA sequence data: ITS1, 2: LN906948, 906950, 906953.

Diagnostic features: Males 4.1–7.6 mm; females 5.1–8.5 mm; buccal capsule short; transverse striations irregular, not prominent; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; spicules 1.13–1.68 mm; spicule ala terminates abruptly just anterior to tip; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.

Comments: *Rugopharynx moennigi* was until recently included within *R. australis*, but was recognised as a sibling species based initially on molecular data (Chilton et al., 2016c; Beveridge et al., 2021). Morphological differences exist in spicule lengths and the gubernaculum, but these can overlap (spicule lengths) or vary (gubernaculum) making the identification of individual specimens from mixed infections problematical (Beveridge et al., 2021)

***Rugopharynx mu* Beveridge & Chilton, 1999**

Rugopharynx mu Beveridge & Chilton, 1999, pp. 825–827, figs 56–65; Aussavy et al., 2011, p. 17; Vendl & Beveridge, 2014, p. 109; Spratt et al., 2017, p. 242; Beveridge, 2016, p. 211.

Type data: holotype SAM AHC 31218, allotype SAM AHC 31219, paratypes SAM AHC 10746, BMNH 1998.6.3.1–2.

Type locality: Teesdale, Vic (38° 01′S 144° 02′E).

Type host: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: Vic, south-eastern NSW; isolated

occurrences in eastern Qld. Map: Beveridge & Chilton, 1999, p. 827.

Representative DNA sequence data: ITS1, 2: LN906969–70.

Diagnostic features (Fig. 36 F): Males 3.8–5.9 mm; females 4.4–6.5 mm; buccal capsule not lobed; transverse striations regular, prominent; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa no longer than lateral lobes; spicules 1.02–1.29 mm; spicule ala terminates abruptly anterior to tip; externo-dorsal ray extremely slender; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.

***Rugopharynx omega* Beveridge, 1982**

Rugopharynx omega Beveridge, 1982, pp. 69–71, figs 238–248; Chilton et al., 1993, p. 159, fig. 16; Beveridge et al., 1994, p. 152; Spratt et al., 2017, p. 241.

Type data: holotype SAM V1758, allotype SAM V1759, paratypes SAM V1760–1767, BMNH 1979.795–799, USNPC 75128.

Type locality: Warwick, Qld (28° 13′S 152° 02′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Other hosts: *Notamacropus parryi* (Bennett, 1835).

Site in host: stomach.

Distribution: south-estern Qld, eastern NSW, eastern Vic. Map: Chilton et al., 1993, p. 162.

Representative DNA sequence data: ITS1, 2: LN906971.

Diagnostic features (Fig. 35 N): Males 3.3–6.8 mm; females 4.8–8.1 mm; buccal capsule prominently trilobed; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; spicules 0.65–0.83 mm; externo-dorsal ray slender; lateral branchlets of dorsal ray arising after principal bifurcation; spicule ala terminating in sharp point at tip; ovejector J-shaped.

***Rugopharynx petrogale* Beveridge & Chilton, 1999**

Rugopharynx petrogale Beveridge & Chilton, 1999, pp. 834–836, figs 90–99.

Rugopharynx australis (in part) Beveridge, 1982, p. 74.

Type data: holotype SAM AHC, 31231, allotype, SAM AHC, 31232, paratypes SAM AHC 14434.

Type locality: Cresbrook Creek, Toowoomba, Qld (27° 34′S 151° 57′E).

Type host: *Petrogale penicillata* (Gray, 1827).

Other hosts: *Petrogale herberti* Thomas, 1926; *Petrogale inornata* Gould, 1842.

Site in host: stomach.

Distribution: eastern Qld. Map: Beveridge & Chilton, 1999, p. 837.

Diagnostic features (Fig. 36 J): Males 5.5–6.8 mm; females 6.1–7.8 mm; buccal capsule short, straight-sided or slightly three-lobed; transverse striations irregular, faint; nerve ring encircles anterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; spicules 0.89–1.05 mm; spicule ala terminates gradually anterior to tip; external branchlets of dorsal ray arising after principal bifurcation; ovejector J-shaped.

Comments: The buccal capsule of this species varies from being almost straight-sided to slightly trilobed and has therefore been included twice in the key. Molecular data are lacking for this species and Beveridge & Chilton (1999) speculated that it might belong to the *R. zeta* complex of species rather than the *R. australis* complex. However, the position of the nerve ring in the anterior oesophageal region suggests a more likely association with the *R. australis* complex.

***Rugopharynx pi* Beveridge & Chilton, 1999**

Rugopharynx pi Beveridge & Chilton, 1999, pp. 817–820; figs 29–38; Aussavy et al., 2011, p. 16; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 241.

Type data: holotype SAM AHC 31226, allotype SAM AHC 31227, paratypes SAM AHC 31228 (incorrectly cited as 31227 in Beveridge & Chilton, 1999), BMNH 1998.6.3.16–21.

Type locality: Brindabella Ranges, NSW (35° 27′S 148° 46′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

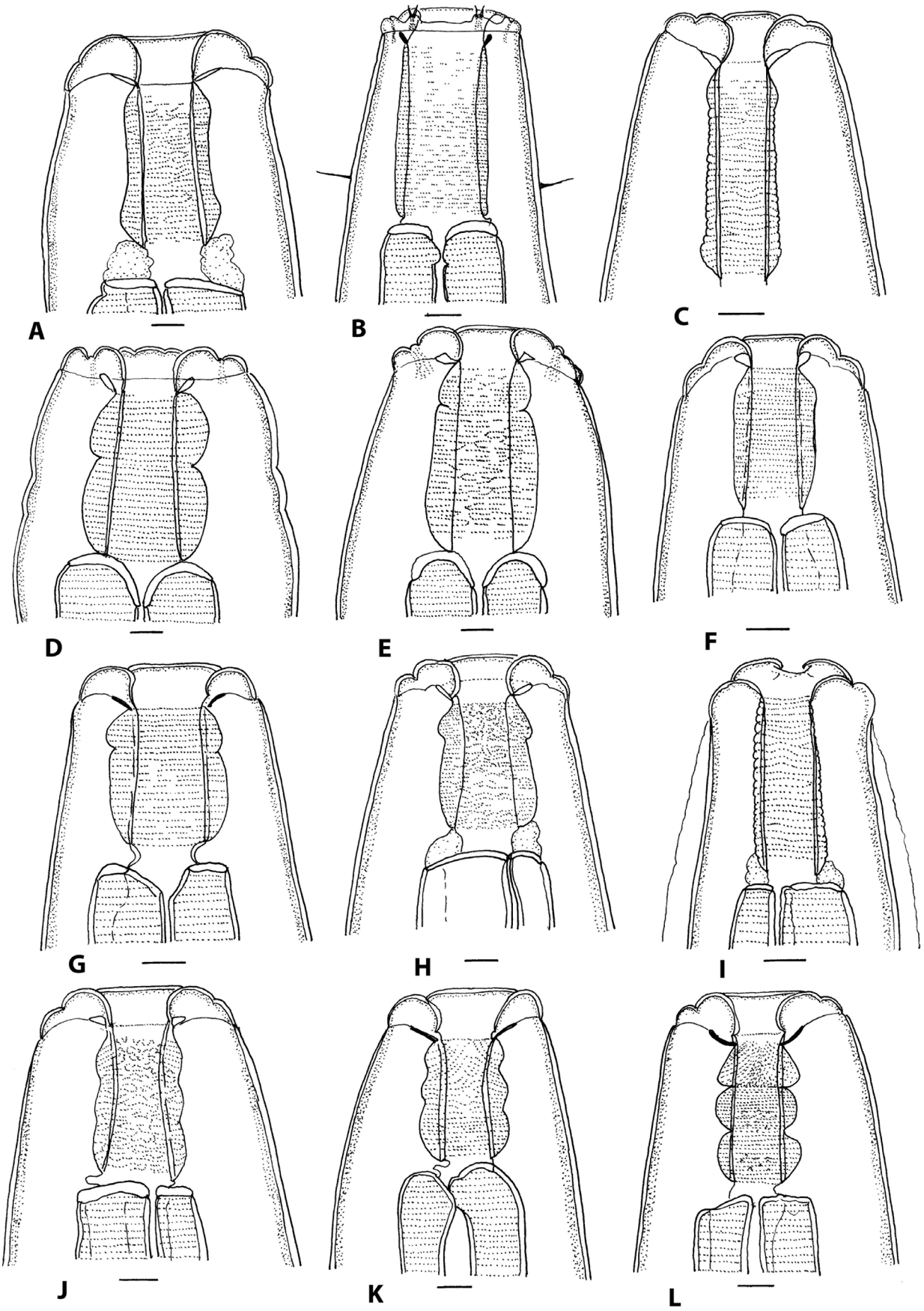
Other hosts: *Notamacropus parryi* (Bennett, 1835).

Site in host: stomach.

Distribution: south-eastern Qld, eastern NSW, western Vic, south-western SA, Tas. Map: Beveridge & Chilton, 1999, p. 819.

Fig. 36. Genus *Rugopharynx*. Optical sections through buccal capsule of species of *Rugopharynx* showing variation in shape and surface patterning. Lateral views, apart from B, which is a dorso-ventral view. A, *Rugopharynx australis*; B, *Rugopharynx rosemariae*; C, *Rugopharynx macropodis*; D, *Rugopharynx epsilon*; E, *Rugopharynx rufogriseus*; F, *Rugopharynx mu*; G, *Rugopharynx chi*; H, *Rugopharynx spratti*; I, *Rugopharynx labiatus*; J, *Rugopharynx petrogale*; K, *Rugopharynx zeta*; L, *Rugopharynx mawsonae*. (A, C, F–H, J, from Beveridge & Chilton, 1999; B, D, E, from Beveridge, 1982; I, from Beveridge, 1999a; K, L, from Beveridge et al., 1994.)

Scale-bars: 0.01 mm.


A
B
C
D
E
F
G
H
I
J
K
L

Representative DNA sequence data: ITS1, 2: LN906972–4.
Diagnostic features: Males 3.6–7.1 mm; females 4.3–8.5 mm; buccal capsule elongate, straight-sided; transverse striations regular, prominent; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; spicules 0.86–1.14 mm; spicule ala diminishing gradually to tip; external branchlets of dorsal ray arising at or immediately after principal bifurcation; ovejector J-shaped.
Comments: Beveridge & Chilton (1999) noted the difficulties in distinguishing this species morphologically from *R. macropodis* in spite of obvious genetic differences. Subtle differences were noted in the bursal bosses and in the proportions of the female tail, but overall size (although overlapping) has been used in the above key as possibly a simpler means of separating the males of the two species. Beveridge & Chilton (1999) expressed reservations about attributing specimens from *N. parryi* to this species. However, subsequent molecular data (Chilton et al., 2016c) have confirmed their conspecificity.

***Rugopharynx rho* Beveridge & Chilton, 1999**

Rugohparynx rho Beveridge & Chilton, 1999, pp. 820–823, figs 39–47.
Type data: holotype SAM AHC 31211, allotype SAM AHC 31212, paratypes SAM AHC 11566.
Type locality: Vivonne Bay, Kangaroo Island, SA (35° 59′S 137° 12′E).
Type host: *Notamacropus eugenii* (Desmarest, 1817).
Site in host: stomach.
Distribution: SA (Kangaroo Island), south-western WA. Map: Beveridge & Chilton, 1999, p. 822, fig. 47, upper figure).
Representative DNA sequence data: ITS1, 2: LN906975–6.
Diagnostic features (Fig. 35 B): Males 8.0–8.9 mm; females 8.7–10.3 mm; buccal capsule elongate, straight-sided; transverse striations regular, faint; nerve ring in anterior oesophageal region; deirid in anterior oesophageal region; dorsal lobe of bursa no longer than lateral lobes; spicules 1.65–1.92 mm; spicule ala diminishing gradually to tip; external branchlets of dorsal ray arising at principal bifurcation; ovejector J-shaped.
Comments: The original description of *R. rho* included *Lago. fasciatus*, *Mac. fuliginosus* and *Pet. lateralis* as additional hosts. The specimens from *Mac. fuliginosus* were subsequently described as an independent species, *R. disiunctus*, while those from *Lago. fasciatus* and *Pet. lateralis* were re–identified as *R. setonicis* (Beveridge, 2020a).

***Rugopharynx rosemariae* Beveridge & Presidente, 1978**

Rugopharynx rosemariae Beveridge & Presidente, 1978, pp. 379–383, figs 1–27; Beveridge & Arundel, 1979, p. 72; Beveridge, 1982, pp. 71–73, figs 249–257; Arundel et al., 1990, p. 42; Aussavy et al., 2011, pp. 14, 15; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 240.
Type data: holotype SAM V1193, allotype SAM V1194, paratypes V1195–1206, BMNH 1979.780–782, USNMHC 75129.
Type locality: Dartmouth, Vic (36° 34′S 147° 35′E).
Type host: *Macropus giganteus* Shaw, 1790.
Other hosts: *Macropus fuliginosus* (Desmarest, 1817).
Site in host: stomach.
Distribution: eastern NSW, Vic, Tas.
Representative DNA sequence data: ITS1, 2: LN906980.
Diagnostic features (Fig. 36 B): Males 7.3–10.4 mm; females 7.6–10.3 mm; buccal capsule elongate, straight-sided, dorso-ventrally compressed; transverse striations regular, faint; oesophageal corpus elongate, lined with spherical bosses; nerve ring in anterior oesophageal region; deirid at level of buccal capsule; dorsal lobe of bursa no longer than lateral lobes; spicules 3.85–4.35 mm; spicule ala terminating abruptly at tip; external branchlets of dorsal ray arising at principal bifurcation; ovejector J-shaped.
Comments: The third-stage larvae of this species are a recognised pathogen in juvenile *Mac. giganteus* (Beveridge & Presidente, 1978; Arundel et al., 1990).

***Rugopharynx rufogriseus* Magzoub, 1964 (orth. emend.)**

Rugopharynx rufogriseus Magzoub, 1964, pp. 49–50, figs 8–12; Beveridge, 1982, pp. 58–59, figs 191–202; Aussavy et al., 2011, p. 16; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 241 (as *rufogrisea*).
Type data: holotype and allotype SAM V1264, paratypes SAM AHC 4917.
Type locality: Logan Village, Qld (27° 46′S 153° 06′E).
Type host: *Notamacropus rufogriseus* (Desmarest, 1817).
Other hosts: *Notamacropus parryi* (Bennett, 1835).
Site in host: stomach.
Distribution: south-eastern Qld, eastern NSW, Vic, south-eastern SA, Tas.
Representative DNA sequence data: ITS1, 2: LN906981–2.
Diagnostic features (Figs 35 D, E, 36 E): Males 3.9–5.3 mm; females 5.0–6.3 mm; buccal capsule short, prominently bilobed with anterior lobe much shorter than posterior lobe; transverse striations irregular, prominent; nerve ring surrounds oesophageal isthmus;

deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; sclerotized bosses on bursa very large; spicules 1.14–1.27 mm; spicule ala terminating abruptly at tip; external branchlets of dorsal ray arising at principal bifurcation; female tail prominently truncated; ovejector J-shaped.

Comments: The original specific name '*rufogrisea*' is grammatically incorrect as the genus *Rugopharynx* is masculine. The orthography is corrected here. Specimens from *N. parryi* (Genbank registration no. LN906983) are genetically distinct from those from *N. rufogriseus* (see Chilton et al., 2016a). However, additional specimens are needed to further investigate these differences.

***Rugopharynx setonicis* Appan, Bergfeld & Beveridge, 2004**

Rugopharynx setonicis Appan, Bergfeld & Beveridge, 2004, pp. 79–80, figs 1–14; Beveridge, 2020a, p. 53.

Type data: holotype SAM AHC 32182, allotype SAM AHC 32183, paratypes SAM AHC 32184, BMNH 2003.2.7.1–2, USNPC 93586.

Type locality: Wellington Dam, WA (33° 24′S 116° 00′E).

Type host: *Setonix brachyurus* (Quoy & Gaimard, 1830).

Other hosts: *Lagostrophus fasciatus* (Péron & Lesueur, 1807); *Petrogale lateralis* Gould, 1840.

Site in host: stomach.

Distribution: WA.

Representative DNA sequence data: ITS1, 2: LN906984.

Diagnostic features: Males 5.3–6.5 mm; females 6.8–7.9 mm; cephalic papillae with single bifid seta; buccal capsule short, with slight lobe at anterior extremity; transverse striations irregular, faint; nerve ring in anterior oesophageal region; deirid post-buccal; dorsal lobe of bursa no longer than lateral lobes; spicules 1.00–1.34 mm; spicule ala terminates gradually anterior to tip; external branchlets of dorsal ray arising at principal bifurcation; ovejector J-shaped.

Comments: Specimens initially identified as *R. rho* from *Lago. fasciatus* and *Pet. lateralis* were reidentified as *R. setonicis* by Beveridge (2020a).

***Rugopharynx sigma* Chilton, Beveridge & Andrews, 1993**

Rugopharynx sigma Chilton, Beveridge & Andrews, 1993, pp. 162–167, figs 3–15; Beveridge et al., 1994, p. 152; Begg et al., 1994, p. 47; Griffith et al., 2000, p. 310.

Type data: holotype SAM V4180, allotype SAM AHC 22873, paratypes SAM AHC 22874.

Type locality: Rumula, Qld (20° 55′S 142° 42′E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Petrogale persephone* Maynes, 1982; *Thylogale calabyi* Flannery, 1992; *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: eastern Qld, PNG. Map: Chilton et al., 1993, p. 163.

Representative DNA sequence data: ITS1, 2: LN906986–7.

Diagnostic features (Figs 35 M, 45 F): Males 5.3–6.9 mm; females 6.4–7.7 mm; buccal capsule prominently trilobed; nerve ring encircles oesophageal isthmus; deirid immediately post-buccal; spicules 0.77–0.90mm; externo-dorsal ray slender; lateral branchlets of dorsal ray arising after principal bifurcation; spicule ala diminishing gradually towards spicule tip; ovejector J-shaped.

***Rugopharynx solitarius* Beveridge, 2020**

Rugopharynx solitarius Beveridge, 2020a, pp. 48–49, 51, figs 25–35.

Type data: holotype SAM AHC 48838, allotype SAM AHC 48839, paratypes SAM AHC 7311.

Type locality: Emuvale, Qld (28° 13′S 152° 14′E).

Type host: *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: south-eastern Qld.

Diagnostic features (Figs 35 G, O): Males 5.1–6.5 mm; females 5.8–6.5 mm; buccal capsule prominently trilobed; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; spicules 1.72–2.15 mm; externo-dorsal ray slender; lateral branchlets of dorsal ray arising after principal bifurcation; elevation of cuticle surrounding lateral branchlets extends almost to extremity of internal branchlets; spicule ala diminishing gradually towards spicule tip; ovejector J-shaped.

***Rugopharynx spratti* Beveridge & Chilton, 1999**

Rugopharynx spratti Beveridge & Chilton, 1999, pp. 827–830, figs 66–74; Aussavy et al., 2011, p. 16; Vendl & Beveridge, 2014, p. 108; Spratt et al., 2017, p. 241.

Type data: holotype SAM AHC 31220, allotype SAM AHC 31221, paratypes SAM AHC 31222, BMNH 1998.6.3.7–15.

Type locality: Brindabella Ranges, NSW (35° 27′S 148° 46′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Site in host: stomach.

Distribution: south-eastern Qld, eastern NSW, Vic, south-eastern SA, Tas. Map: Beveridge & Chilton, 1999, p. 829.

Representative DNA sequence data: ITS1, 2: LN906988–9.
Diagnostic features (Figs 36 H, 45 G): Males 5.6–8.5 mm; females 6.9–9.5 mm; buccal capsule short, with prominent lobe at anterior extremity; transverse striations irregular, prominent; nerve ring at oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; spicules 1.27–1.78 mm; spicule ala terminates abruptly anterior to tip; external branchlets of dorsal ray arising at principal bifurcation; ovejector J-shaped.

***Rugopharynx tau* Beveridge & Chilton, 1999**

Rugopharynx tau Beveridge & Chilton, 1999, pp. 832–843, figs 83–89; Griffith et al., 2000, p. 310.
Type data: holotype SAM AHC 31213, allotype SAM AHC 31214, paratypes SAM AHC 8132, BMNH 1998.6.3.3–4.
Type locality: Dorrigo, NSW (30° 23'S 152° 51'E).
Type host: *Thylogale thetis* (Lesson, 1827).
Other hosts: *Thylogale stigmatica* (Gould, 1860).
Site in host: stomach.
Distribution: south-eastern Qld, north-eastern NSW. Map: Beveridge & Chilton, 1999, p. 833.
Representative DNA sequence data: ITS1, 2: LN906990.
Diagnostic features: Males 4.6–6.4 mm; females 6.0–7.9 mm; buccal capsule short, mildly lobed at anterior and posterior extremities; transverse striations irregular, faint; nerve ring asurrounds oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa longer than lateral lobes; spicules 1.19–1.57 mm; spicule ala terminates abruptly anterior to tip; external branchlets of dorsal ray arising at principal bifurcation; ovejector J-shaped.

***Rugopharynx theta* (Johnston & Mawson, 1939)**

Pharyngostrongylus theta Johnston & Mawson, 1939b, p. 514, figs 1–2; 1939d, p. 307; 1940a, pp. 468–469; Popova 1958, pp. 249–259, fig. 169.
Rugopharynx theta: Yamaguti, 1961, p. 410; Mawson, 1965, p. 153, figs 31–36; Beveridge, 1982, pp. 79–81, figs 272–279; Beveridge et al., 1998, p. 482.
Type data: holotype SAM V1368.
Type locality: New England, NSW.
Type host: *Thylogale thetis* (Lesson, 1827) (probable misidentification of *N. dorsalis* (Gray, 1837).
Other hosts: *Notamacropus dorsalis* (Gray, 1837); unconfirmed host: *Notamacropus rufogriseus* (Desmarest, 1817).
Site in host: stomach.
Distribution: eastern Qld, north-eastern NSW.
Representative DNA sequence data: ITS1, 2: LN906992.
Diagnostic features: Males 2.6–4.9 mm; females 4.5–5.5 mm; cephalic collar subdivided into four lobes; buccal capsule elongate mildly lobed at anterior and posterior extremities; transverse striations regular, prominent; nerve ring surrounds oesophageal isthmus; deirid in anterior oesophageal region; dorsal lobe of bursa no longer than lateral lobes; bursa without sclerotized bosses; spicules 1.60–2.09 mm; spicule ala terminates abruptly anterior to tip; external branchlets of dorsal ray rudimentary, arising at principal bifurcation; ovejector J-shaped.
Comments: This is the only species within the genus to lack sclerotised bosses on the bursa. Together with *R. labiatus*, it has the labial collar subdivided into four sectors. The type host, *Thyl. thetis*, is apparently a host misidentification for *N. dorsalis* (Beveridge, 1982, p. 81) and there are no additional records to support the finding of the species in *N. rufogriseus* (Johnston & Mawson, 1939c).

***Rugopharynx thetidis* Beveridge, 2020**

Rugopharynx thetidis Beveridge, 2020a, pp. 42–43, figs 1–13.
Type data: holotype SAM AHC 48776, allotype SAM AHC 48777, paratypes SAM AHC 48778.
Type locality: Lamington National Park, Qld (28° 08'S 153° 06'E).
Type host: *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: south-eastern Qld, north-eastern NSW.
Representative DNA sequence data: ITS1, 2: LN906985.
Diagnostic features (Fig. 35 L): Males 4.1–5.6 mm; females 6.0–7.2 mm; buccal capsule prominently trilobed; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; spicules 0.68–0.80 mm; externo-dorsal ray slender; lateral branchlets of dorsal ray arising after principal bifurcation; spicule tip prominently hooked; ovejector J-shaped.

***Rugopharynx thylogale* Beveridge, 2020**

Rugopharynx thylogale Beveridge, 2020a, pp. 45–47, figs 14–24.
Type data: holotype SAM AHC 48779, allotype SAM AHC 48780, paratypes SAM AHC 30907, BMNH 2019.8.12.17–23.
Type locality: Lamington National Park, Qld (28° 08'S 153° 06'E).
Type host: *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.
Distribution: south-eastern Qld.
Diagnostic features (Fig. 35 H): Males 4.7–5.1 mm; females 4.9–5.6 mm; buccal capsule prominently trilobed; nerve ring encircles oesophageal isthmus; deirid immediately post-buccal; spicules 1.07–1.23 mm; externo-dorsal ray slender; lateral branchlets of dorsal ray arising after principal bifurcation; dorsal lobe elongate, external branchlets of dorsal ray twice as long as trunk; spicule ala diminishes gradually in width towards tip; ovejector J-shaped.

***Rugopharynx zeta* (Johnston & Mawson, 1939)**

Pharyngostrongylus zeta Johnston & Mawson, 1939a, pp. 138–139, figs 47–50; Popova, 1958, p. 250.
Rugopharynx zeta: Yamaguti, 1961, p. 410; Wahid, 1964, p. 188; Beveridge, 1982, pp. 60–63, figs 213–216; Beveridge et al., 1989, p. 277; 1994, pp. 163–165, figs 1–12; 1995, p. 152.
Type data: holotype and allotype SAM V1555.
Type locality: Upper Burnett River, Qld (24° 54′S 152° 23′E).
Type host: *Petrogale herberti* Thomas, 1926.
Other hosts: *Petrogale assimilis* Ramsay, 1877; *Petrogale inornata* Gould, 1842; *Petrogale mareeba* Eldridge & Close, 1992; *Petrogale penicillata* (Gray, 1827); *Petrogale sharmani* Eldridge & Close, 1992.
Site in host: stomach.
Distribution: eastern Qld. Map: Beveridge et al., 1994, p. 169.
Representative DNA sequence data: ITS1, 2: LN906992–4.
Diagnostic features (Figs 35 C, 36 K, 45 H): Males 4.9–6.6 mm; females 5.9–6.7 mm; buccal capsule slightly to prominently trilobed; nerve ring encircles oesophageal isthmus; deirid in anterior oesophageal region; spicules 1.57–1.75 mm; externo-dorsal ray slender; lateral branchlets of dorsal ray arising after principal bifurcation; spicule ala terminates abruptly at tip; ovejector J-shaped.
Comments: Unsubstantiated records in *N. rufogriseus* and *Thyl. thetis* were listed by Spratt & Beveridge (2016). These records predate the taxonomic separation of *R. omega* and *R. solitarius* from *R. zeta* and the records probably belong to these two host species. The shape of the buccal capsule is more variable in *R. zeta* than in most other species, sometimes being only slightly trilobed. For this reason it has been included in the key to species twice.

Rugostrongylus Beveridge, 1982

Type and only species*: Rugostrongylus labiatus* (Davey & Wood, 1938).

Generic diagnosis: cephalic collar present; cephalic papillae dome-shaped with paired, subequal setae; labial collar present; labial crown absent; mouth opening and buccal capsule dorsoventrally elongate; buccal capsule elongate, sclerotized with transverse striations; deirid at level of buccal capsule; oesophageal corpus elongate; oesophageal bulb elongate, sub-cylindrical; anterior extremity of intestine projects anteriorly with dorsal and ventral lobes enveloping posterior region of oesophageal bulb; bursa with bosses on surface; spicules elongate, alate; gubernaculum absent; ovejector J-shaped.

***Rugostrongylus labiatus* (Davey & Wood, 1938)**

Macropostrongylus labiatus Davey & Wood, 1938, p. 263, figs 9, 10.
Gelanostrongylus labiatus: Popova, 1960, pp. 87–88, fig. 56.
Zoniolaimus labiatus: Mawson, 1977b, p.51.
Rugostrongylus labiatus: Beveridge, 1982, pp. 48–50, figs 156–166; Beveridge et al., 1998, p. 482.
Type data: syntypes QM GL12154; BMNH 1939.1.10.131–134.
Type locality: Yabulu, Qld (19° 12′S 146° 36′E).
Type host: *Osphranter robustus* (Gould, 1840) (probably an error for *N. parryi* (Bennett, 1835)).
Other hosts: *Notamacropus parryi* (Bennett, 1835).
Site in host: stomach.
Distribution: northern NSW, Qld.
Representative DNA sequence data: ITS1, 2: MG865639.
Diagnostic features (Figs 37 A–D): Males 7.9–8.7 mm, females 7.8–10.9 mm; cephalic collar and labial collar present; labial crown absent; cephalic papillae with paired elongate setae; mouth opening and buccal capsule dorsoventrally elongate; buccal capsule elongate, cylindrical with numerous, faint transverse striations; single, flap-like valve at posterior end of buccal capsule; oesophagus elongate; anterior intestinal cells enlarged; bursa with sclerotized bosses; spicules 2.52–2.89 mm; ovejector J-shaped.
Comments: This distinctive species was first described from *O. robustus* (see Davey & Wood, 1938) but has never since been found in this host species (Beveridge, 2020c). However, the species is common in *N. parryi* (see Beveridge, 1982; Beveridge et al., 1998) suggesting that the identification of the type host is in error.

Sacculostrongulus n. gen.

Type and only species: *S. ochetocephalus* (Beveridge, 1986) n.comb.

Generic definition: cephalic collar present; mouth opening dorso-ventrally elongate; cephalic papillae conical with paired setae; amphids prominent; buccal capsule slightly wider than long, poorly sclerotized, without transverse striations; walls of buccal capsule supported externally by prominent radial musculature; anterior extremity of buccal capsule with 8 lip-like protrusions into lumen of capsule; 8 tubular structures in 4 submedian pairs run from level of buccal capsule almost to nerve ring; oesophageal corpus elongate, isthmus indistinct, bulb fusiform; nerve ring in anterior oesophageal region; deirid posterior to buccal capsule; excretory pore posterior to oesophago-intestinal junction; anterior extremity of intestine expanded but not enclosing oesophageal bulb; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum absent; vulva immediately anterior to anus; ovejector J-shaped.

Comments: This species was allocated to the genus *Monilonema* on the basis of the presence of tubular structures extending from the anterior extremity to the mid-oesophageal region, potentially a unique morphological synapomorphy with *Mo. lacunosum* (Beveridge et al., 2020). However, molecular data (Chilton et al., 2018; Beveridge et al., 2020) by contrast clearly separated these two species, with the type species, *Mo. lacunosum*, aligned with the genera *Rugopharynx* and *Thallostonema*, and with *S. ochetocephalus* aligned with genera of the tribe Macropostrongylinea. In reviewing the other morphological features, the molecular associations are supported by other morphological data. *Sacculostrongylus ochetocephalus* has a number of morphological affinities with the Macropostrongylinea including the eight lobes at the mouth opening, the strong muscular supports for the buccal capsule and the lack of bursal bosses. By contrast, *Mo. lacunosum*, with a leaf crown-like flange at the anterior extremity of the buccal capsule and a bursa with bosses is more closely aligned morphologically with the *Rugopharynx/Thallostonema* clade. For these reasons, a new genus has been erected for *Mo. ochetocephalum*.

Sacculostrongylus ochetocephalus (Beveridge, 1986) n.comb.

Monilonema ochetocephalum Beveridge, 1986, pp. 251–254, fig 1A–M (as *ochetocephala*); Beveridge et al., 1998, p. 483.

Type data: holotype SAM V3578, allotype SAM V3579, paratypes SAM V3850–3583, AHC 13462–13466, MNHNP 532 HD.

Type locality: Harvest Home Station via Charters Towers, Qld (20° 42′S 146° 38′E).

Type host: *Notamacropus dorsalis* (Grey, 1837).

Other hosts: *Wallabia bicolor* (Desmarest, 1804).

Site in host: stomach.

Distribution: Qld, NSW.

Representative DNA sequence data: ITS1, 2: HE775537.

Diagnostic features (Figs 37 E–I): Males 8.0–9.4 mm; females 10.6–14.7 mm; spicules 1.60–180 mm; vagina very short, 0.55–0.70; ovejector J-shaped.

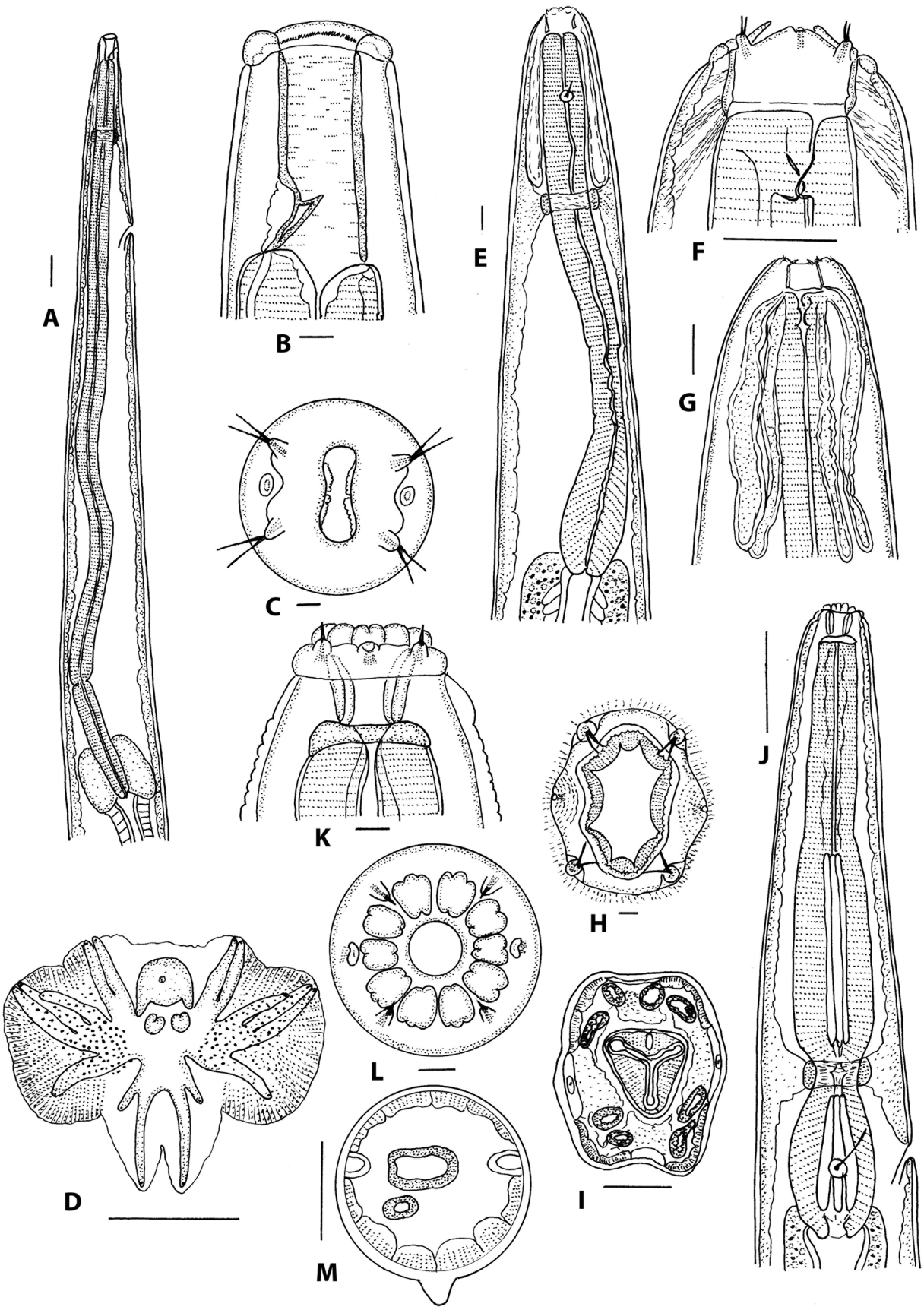
Spirostrongylus Yorke & Maplestone, 1926

Type and only species: *Spirostrongylus spirostrongylus* Yorke & Maplestone, 1926.

Generic definition: nematodes coiled dextrally; ventral ala extends full length of body; cephalic collar present; labial collar of 10 rounded lobes; cephalic papillae dome-shaped with single seta; buccal capsule heavily sclerotized, circular in cross section, cup-shaped, non-striated; oesophageal corpus with narrower

Fig. 37. Genera *Rugostrongylus*, *Sacculostrongylus* n.g. and *Spirostrongylus*. A, *Rugostrongylus labiatus*, oesophagus, lateral view; B, *Ru. labiatus*, buccal capsule, lateral view; C, *Ru. labiatus*, anterior end, apical view; D, *Ru. labiatus*, bursa, apical view; E, *Sacculostrongylus ochetocephalus,* oesophagus, lateral view; F, *S. ochetocephalus*, buccal capsule, lateral view; G, *S. ochetocephalus*, anterior end showing tubular structures; H, *S. ochetocephalus*, anterior end, apical view; I, *S. ochetocephalus*, transverse section through anterior end showing eight tubular structures; J, *Spirostrongylus spirostrongylus*, oesophagus, lateral view; K, *S. spirostrongylus*, buccal capsule, lateral view; L, *S. spirostrongylus*, anterior end, apical view; M, *S. spirostrongylus*, transverse section through body showing ventral ala. (A–D, J–M from Beveridge, 1982; E–I from Beveridge, 1986c).

Scale-bars: A, D–G, I–M, 0.1 mm; B, C, H, 0.01 mm.


A
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anterior section and broader posterior section; oesophageal bulb ovoid with 3 pairs of sclerotized plates in lining; nerve ring at level of oesophageal isthmus; deirid and excretory pore at level of oesophageal bulb; bursa with non-sclerotized bosses; spicules elongate, alate; gubernaculum present vulva immediately anterior to anus; ovejector J-shaped.

***Spirostrongylus spirostrongylus* Yorke & Maplestone, 1926**

Spirostrongylus spirostrongylus Yorke & Maplestone, 1926, p. 70, fig. 36; Popova, 1958, pp. 267–268, fig. 181; Beveridge, 1982, pp. 84–87, figs 290–303; Speare et al., 1983, p. 90; Beveridge et al., 1998, p. 483.

Type data: "cotypes" SAM AHC 6155, BMNH 1927.7.21.13–16.

Type locality: Townsville, Qld (19° 15'S 146° 49'E).

Type host: *Notamacropus agilis* (Gould, 1842) (as *Macropus* sp.).

Other hosts: *Notamacropus parryi* (Bennett, 1835).

Site in host: oesophagus.

Distribution: Qld, NT.

Representative DNA sequence data: ITS1, 2: LN846149.

Diagnostic features (Figs 37 J–M): Males 5.8–8.2 mm; females 7.1–10.5 mm; spicules 0.90–1.20 mm; dorsal ray divides close to origin; J-shaped ovejector.

Comments: *Spirostrongylus spirostrongylus* is primarily a parasite of *N. agilis*, but also occurs in *N. parryi* in areas where the two species of wallaby are sympatric (Beveridge, 1982; Beveridge et al., 1998).

Tethystrongylus Beveridge, 1983

Type and only species: *Tethystrongylus coronatus* Beveridge, 1983.

Generic definition: cephalic collar absent; cephalic papillae domed, armed with single, short seta; mouth opening circular; external leaf crown present, composed of numerous tiny elements; buccal capsule cylindrical, much longer than wide, moderately sclerotized, with numerous irregular transverse striations; oesophageal corpus elongate without accessory fusiform bulb in mid-oesophageal region; terminal bulb ovoid, lined with 3 pairs of elongate sclerotized plates; nerve ring in anterior oesophageal region; excretory pore and deirids at level of nerve ring; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum absent; ovejector J-shaped.

***Tethystrongylus coronatus* Beveridge, 1983**

Tethystrongylus coronatus Beveridge, 1983, pp. 54–55, figs 205–213, 222; Griffith et al., 2000, p. 310; Spratt & Beveridge, 2016, p. 161.

Type data: holotype SAM V2981, allotype SAM V2982, paratypes SAM V2983–2985, SAM AHC 11352, BMNH 1981.3686–3687, USNPC 76630.

Type locality: Emu Vale, Qld (28° 14'S 152° 15'E).

Type host: *Thylogale thetis* (Lesson, 1827).

Other hosts: *Thylogale calabyi* Flannery, 1992.

Site in host: stomach.

Distribution: south-eastern Qld; PNG.

Diagnostic features (Figs 38 A–D): Males 8.6–11.5 mm; females 12.9–16.3 mm; spicules 2.71–2.96 mm; ovejector J-shaped.

Thallostonema Beveridge, 1983

Type species: *Thallostonema lichtenfelsi* Beveridge, 1983.

Other species: *Th. kirkpatricki* Beveridge, 1983; *Th. queenslandense* Beveridge, 1983; *Th. rarum* Beveridge, 1983; *Th. setifer* (Johnston & Mawson, 1939); *Th. thylogalarum* Beveridge, 1983.

Generic definition: cephalic collar vestigial or absent; lips absent; submedian papillae dome-shaped, with single seta, occasionally bifid; mouth opening circular, trapezoidal or dorsoventrally elongate; teeth arising from anterior extremity of buccal capsule; buccal capsule strongly sclerotised with irregular transverse striations; oesophageal corpus broader than remaining oesophagus; posterior oesophagus slender, elongate; nerve ring at posterior end of oesophageal corpus; excretory pore at level of nerve ring; deirids in region of buccal capsule; bursa with sclerotized bosses; spicules elongate, alate; gubernaculum present; ovejector J-shaped.

Comments: Several of the new specific names erected by Beveridge (1983) were incorrectly given feminine endings; the genus is neuter and the endings have subsequently been corrected (Spratt & Beveridge, 2016). The species of this genus can often be identified based on the shape of the buccal capsule and the setae on the cephalic papillae. However, the morphology of the mouth opening can also be highly informative and, although more difficult to examine, has been included in the illustrations. The genus is immediately recognisable from the shape of the oesophagus.

Key to species of Thallostonema

1a. Setae on submedian cephalic papillae bifid (Figs 38 H, J, N) 2
1b. Setae on submedian cephalic papillae single (Figs 38 K–M) 3

2a. Spicules < 1.8 mm . . . . . *Th. setifer*
2b. Spicules > 2.2 mm . . . . . *Th. rarum*

3a. Buccal capsule much longer than wide (Fig. 38 I) 4
3b. Buccal capsule only slightly longer than wide (Fig 38 J) 5

4a. Spicules > 2.8 mm; 8 perioral teeth present . . . . . *Th. kirkpatricki*
4b. Spicules > 1.8 mm; 16 perioral teeth present (Fig. 38 K) . . . . . *Th. lichtenfelsi*

5a. Lateral branchlets of dorsal ray arising well after primary bifurcation. . . . *Th. thylogalarum*
5b. Lateral branchlets of dorsal ray arising at or anterior to primary bifurcation . . . . . *Th. queenslandense*

***Thallostonema kirkpatricki* Beveridge, 1983**

Thallostonema kirkpatricki Beveridge, 1983, pp. 45–46, figs 155–162, 226; Griffith et al., 2000, p. 310.
Type data: holotype SAM V3020, allotype SAM V3021, paratypes SAM V3022–3023, BMNH 1981.3704–3705, USNPC 76635.
Type locality: Emu Vale, Qld (28° 14′S 152° 15′E).
Type host: *Thylogale thetis* (Lesson, 1827).
Other hosts: *Thylogale stigmatica* (Gould, 1860).
Site in host: stomach.
Distribution: south-eastern Qld.
Representative DNA sequence data: ITS1, 2: MG865640.
Diagnostic features (Fig. 38 I): Males 5.4–8.3 mm; females 6.3–11.0 mm; cephalic papillae with single seta; mouth opening oval; 2 large dorsal and ventral blunt-tipped teeth; 4 submedian smaller blunt-tipped teeth; buccal capsule much longer than wide; spicules 2.90–3.40 mm; spicular ala terminates abruptly anterior to spicule tip; ovejector J-shaped.

***Thallostonema lichtenfelsi* Beveridge, 1983**

Thallostonema lichtenfelsi Beveridge, 1983, pp. 43–45, figs 145–154, 225; Beveridge et al., 1992, p. 364; Griffith et al., 2000, p. 310.
Type data: holotype SAM V3008, allotype SAM V3009, paratypes SAM V3010–3019, SAM AHC 11370, BMNH 1981.3698–3703, USNPC 76634.
Type locality: Tolga, Qld (17° 13′S 145° 29′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Other hosts: *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: eastern Qld.
Representative DNA sequence data: ITS1, 2: MG865641.
Diagnostic features (Figs 38 D, F, K): Males 6.5–8.4 mm; females 8.3–10.3 mm; cephalic papillae with single seta; mouth opening circular; 2 large dorsal and ventral blunt-tipped teeth; 4 submedian smaller blunt-tipped teeth; 8 small, sharp-tipped teeth either side of each sub-median tooth; buccal capsule much longer than wide; spicules 1.46–1.72 mm; spicular ala diminishes gradually towards spicule tip; ovejector J-shaped.

***Thallostonema queenslandense* Beveridge, 1983**

Thallostonema queenslandense Beveridge, 1983, pp. 48–50, figs 175–184 (as *queenslandensis*); Beveridge et al., 1989, p. 277; Begg et al., 1995, p. 47.
Type data: holotype SAM V3036, allotype SAM V3037, paratypes SAM V3038–3042, SAM AHC 11335, BMNH 1981.3708–3709, USNPC 76637.
Type locality: Proserpine, Qld (20° 24′S 148° 35′E).
Type host: *Petrogale persephone* Maynes, 1982.
Site in host: stomach.
Distribution: north-eastern Qld.
Representative DNA sequence data: ITS1, 2: MG865642.
Diagnostic features (Figs 38 G, M): Males 5.2–6.3 mm; females 6.0–7.3 mm; cephalic papillae with single seta; mouth opening dorsoventrally elongate; 2 large dorsal and ventral blunt-tipped teeth; tiny paired teeth associated with each submedian papilla; single tiny tooth associated with each amphid; buccal capsule slightly longer than wide; spicules 1.62–1.81 mm; ovejector J-shaped.

***Thallostonema rarum* Beveridge, 1983**

Thallostonema rarum Beveridge, 1983, pp. 52–53, figs 197–205 (as *rara*).
Type data: holotype SAM V3043.
Type locality: Swanfels, Qld (28° 11′S 141° 551′E).
Type host: *Notamacropus rufogriseus* (Desmarest, 1817).
Site in host: stomach.
Distribution: south-eastern Qld.
Representative DNA sequence data: ITS1, 2: MG865643.
Diagnostic features (Fig. 38 J): Males 6.1–7.6 mm; cephalic papillae with single bifid seta; mouth opening quadrangular; 4 rounded teeth in median and lateral

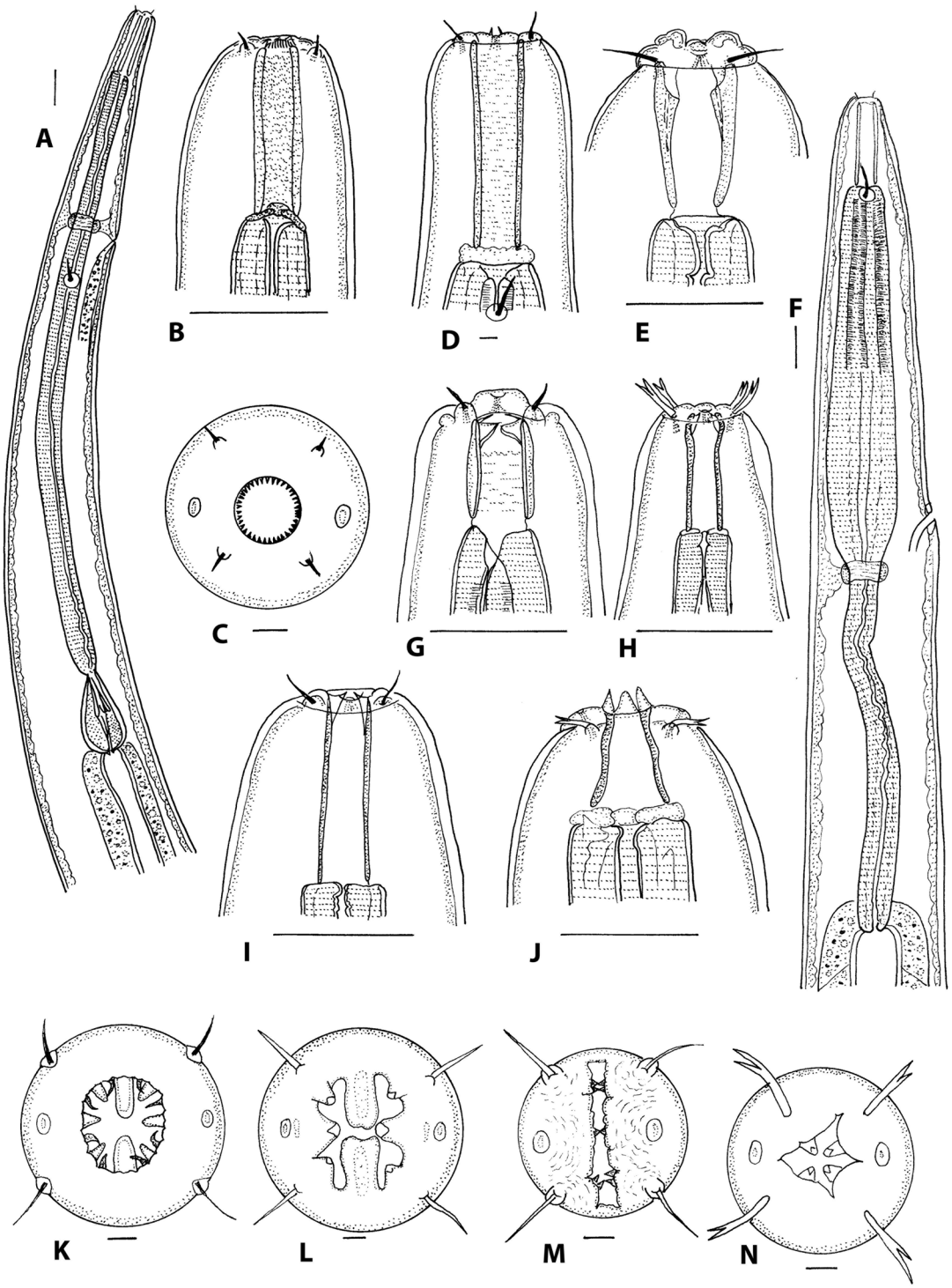


Fig. 38. Genera *Tethystrongylus*, *Thallostonema*. A, *Tethystrongylus coronatus*, anterior end, lateral view; B, *T. coronatus*, buccal capsule, lateral view; C, *T. coronatus*, anterior end, apical view; D, *Thallostonema lichtenfelsi*, buccal capsule, lateral view; E, *Th. thylogalarum*, buccal capsule, lateral view; F, *Th. lichtenfelsi*, anterior end, lateral view; G, *Th. queenslandense*, buccal capsule, lateral view; H, *Th. setifer*, buccal capsule, lateral view; I, *Th. kirkpatricki*, buccal capsule, lateral view; J, *Th. rarum*, buccal capsule, lateral view; K, *Th. lichtenfelsi*, anterior end, apical view; L, *Th. thylogalarum*, anterior end, apical view; M, *Th. queenslandense*, anterior end, apical view; N, *Th. setifer*, anterior end, apical view (from Beveridge, 1983).

Scale-bars: A, B, E–J, 0.1 mm; C, D, K–N, 0.01 mm.

positions; 4 tiny teeth in submedian positions; buccal capsule slightly longer than wide; spicules 2.31–2.34 mm.

Comments: This species is currently inadequately described in lacking the description of the female.

***Thallostonema setifer* (Johnston & Mawson, 1939)**

Buccostrongylus setifer Johnston & Mawson, 1939b, pp. 527–529, figs 39–41; 1939c, p. 308; Kung, 1948, pp. 105–106; Skrjabin et al., 1952, p. 164, fig. 80; Popova, 1960, pp. 37–38, fig. 25; Yamaguti, 1961, p. 404.

Zoniolaimus chaetophorus: Johnston & Mawson, 1949, p. 66.

Thallostonema setifer: Beveridge, 1983, pp. 50–52, figs 185–196; Spratt et al., 2017, p. 241 (as *setiferum*).

Type data: holotype SAM V 2815, allotype SAM V2816, paratypes SAM AHC 2927.

Type locality: Bathurst, NSW (33° 25'S 149° 35'E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Site in host: stomach.

Distribution: Qld, NSW, Vic, Tas.

Representative DNA sequence data: ITS1, 2: MG865644–46.

Diagnostic features (Fig. 38 N): Males 4.2–5.1 mm; females 5.3–6.6 mm; cephalic papillae with single bifid seta; mouth opening trapezoidal; 4 large submedian teeth; buccal capsule longer than wide, campanulate at anterior end; spicules 1.60–1.81 mm; spicule ala terminates abruptly anterior to spicule tip; ovejector J-shaped.

Comments: The specific epithet was cited as '*setifer*' by Beveridge (1983) and as '*setiferum*' by Spratt & Beveridge (2016) and Spratt et al. (2017). This difficulty arises as 'setifer' can be either a noun (carrying a seta) or an adjective. The original authors of the name gave no indication as to how they used this name. If it was used as a noun in apposition it remains as '*setifer*' when transferred to *Thallostonema*. If it was used as an adjective, it becomes '*setiferum*' as used by Spratt & Beveridge (2016) and Spratt et al. (2017).

***Thallostonema thylogalarum* Beveridge, 1983**

Thallostonema thylogalarum Beveridge, 1983, pp. 47–48, figs 163–174, 227; Griffith et al., 2000, p. 310.

Type data: holotype SAM V3024, allotype SAM V3025, paratypes SAM V3026–3035, BMNH 1981.3706–3707; USNPC 76636.

Type locality: Emu Vale, Qld (28° 14'S 152° 15'E).

Type host: *Thylogale thetis* (Lesson, 1827).

Other hosts: *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: south-eastern Qld; north-eastern NSW.

Representative DNA sequence data: ITS1, 2: MG865647.

Diagnostic features (Figs 38 E, L): Males 4.1–7.7 mm; females 4.9–8.1 mm; cephalic papillae with single seta; mouth opening dorsoventrally elongate; 2 large dorsal and ventral blunt-tipped teeth; 6 teeth associated with each submedian papilla and amphid; buccal capsule longer than wide; spicules 1.45–2.04 mm; spicule ala terminates abruptly anterior to spicule tip; ovejector J-shaped.

Thylicostrongylus n. gen.

Type species: *Thylicostrongylus thylogale* (Beveridge, 1983) n.comb.

Other species: *Ty. gallardi* (Johnston & Mawson, 1939) n.comb.; *Ty. parvispicularis* (Beveridge, 1983) n. comb.; *Ty. tasmaniensis* (Beveridge, 1983) n. comb.; *Ty. macropodis* Beveridge, 2020 n.comb.

Generic definition: Cephalic collar present; cephalic papillae domed, armed with single, bifid or paired setae; mouth opening circular, with 4 lips without pulp cavities, in dorsal, ventral and lateral positions; interlabia absent; buccal capsule cylindrical, moderately sclerotized, lacking transverse striations; oesophagus without accessory fusiform bulb; terminal bulb ovoid, lined with 3 pairs of elongate sclerotized plates; nerve ring at level of oesophageal isthmus; excretory pore at level of nerve ring (except in *Ty. thylogale*); bursa without sclerotized bosses; spicules elongate, alate; gubernaculum absent; ovejector J-shaped.

Comments: Species of *Thylicostrongylus* were formerly placed in the genus *Wallabinema* (Beveridge, 1983, 2020b). However, the molecular data of Chilton et al. (2018) and Beveridge et al. (2020) suggested that the genus was para- or polyphyletic and this group of species had already been identified as morphologically distinctive based primarily on the position of the nerve ring (Fig. 40 D). In addition, they are primarily parasites of *Thylogale* spp. This group of species has therefore been separated from *Wallabinema*, with the new generic name indicating their occurrence primarily in *Thylogale* spp. The species are most readily differentiated from one another based on spicule lengths.

Key to species of Thylicostrongylus

1a. Spicules > 1.5 mm . . . . . *Ty. gallardi*
1b. Spicules < 1.5 mm 2

2a. Spicules > 0.90 mm . . . . . *Ty. macropodis*
2b. Spicules < 0.90 mm 3

3a. Spicules > 0.60 mm . . . . . *Ty. thylogale*
3b. Spicules < 0.60 mm 4

4a. Spicules > 0.40 mm . . . . . *Ty. tasmaniensis*
4b. Spicules < 0.30 mm . . . . . *Ty. parvispicularis*

***Thylicostrongylus gallardi* (Johnston & Mawson, 1939) n. comb.**

Cyclostrongylus gallardi Johnston & Mawson, 1939b, p. 518, figs 11–13; Popova, 1960, pp. 79–80, fig. 49; Mawson, 1977a, pp. 19–20; Beveridge, 1982, p. 88.

Wallabinema gallardi: Beveridge, 1983, pp. 41–42, figs 140–144; Griffith et al., 2000, p. 310; Beveridge, 2020b, pp. 64–65, figs 18–26, 28.

Type data: holotype and allotype SAM V1561.

Type locality: Ourimbah, NSW (29° 17′S 143° 39′E).

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Other hosts: *Thylogale stigmatica* Gould, 1860; *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: south-eastern Qld, north-eastern NSW.

Diagnostic features: Males 4.8–5.2 mm; females 4.8–5.8 mm; cephalic collar present; cephalic papillae domed with single short seta, bifid at tip; 4 small, triangular lips, dorsal, ventral and 2 lateral, without pulp cavity, forming a labial collar; buccal capsule cylindrical in lateral view, slightly longer than wide; oesophageal corpus about 5 times as long as bulb; nerve ring at level of oesophageal isthmus; spicules 0.97–1.17 mm; female tail 0.24–0.47 mm; ovejector J-shaped.

Comments: This species has not been found in *N. rufogriseus* since its original description. However, given its prevalence in *Thyl. thetis*, it is possible that there was some confusion in naming the original host species, with the common name of *N. rufogriseus*, the red-necked wallaby, being readily mistaken for that of *Thyl. thetis*, being the red-necked pademelon.

***Thylicostrongylus macropodis* (Beveridge, 2020) n. comb.**

Wallabinema macropodis Beveridge, 2020b, pp. 60–64, figs 10–17, 27.

Type data: holotype SAM AHC 48844, allotype SAM AHC 48845, paratypes SAM AHC 48846.

Type locality: Forty Mile Scrub National Park, Qld (18° 06′S 144° 45′E).

Type host: *Notamacropus dorsalis* (Gray, 1837).

Other hosts: *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: eastern Qld.

Representative DNA sequence data: ITS1, 2: MN864141.

Diagnostic features: Male 3.6–4.6 mm; female 4.6–5.7 mm; cephalic collar present; cephalic papillae domed with single short seta; 4 domed lips, dorsal, ventral and 2 lateral, without pulp cavity; buccal capsule cylindrical, slightly long than wide; oesophageal corpus about 5 times as long as bulb; nerve ring at level of oesophageal isthmus; spicules 0.97–1.17 mm; spicule tip simple; spicule ala diminishes in width towards spicule tip; female tail 0.24–0.37 mm; ovejector J-shaped.

Comments: All of the morphologically related species (*Ty. gallardi*, *Ty. parvispicularis*, *Ty. tasmaniense* and *Ty. thylogale*) are parasites of *Thylogale* spp. It seems likely that the usual host of this species may also be a species of *Thylogale* spp. but in this instance was found also in the sympatric species *N. dorsalis*.

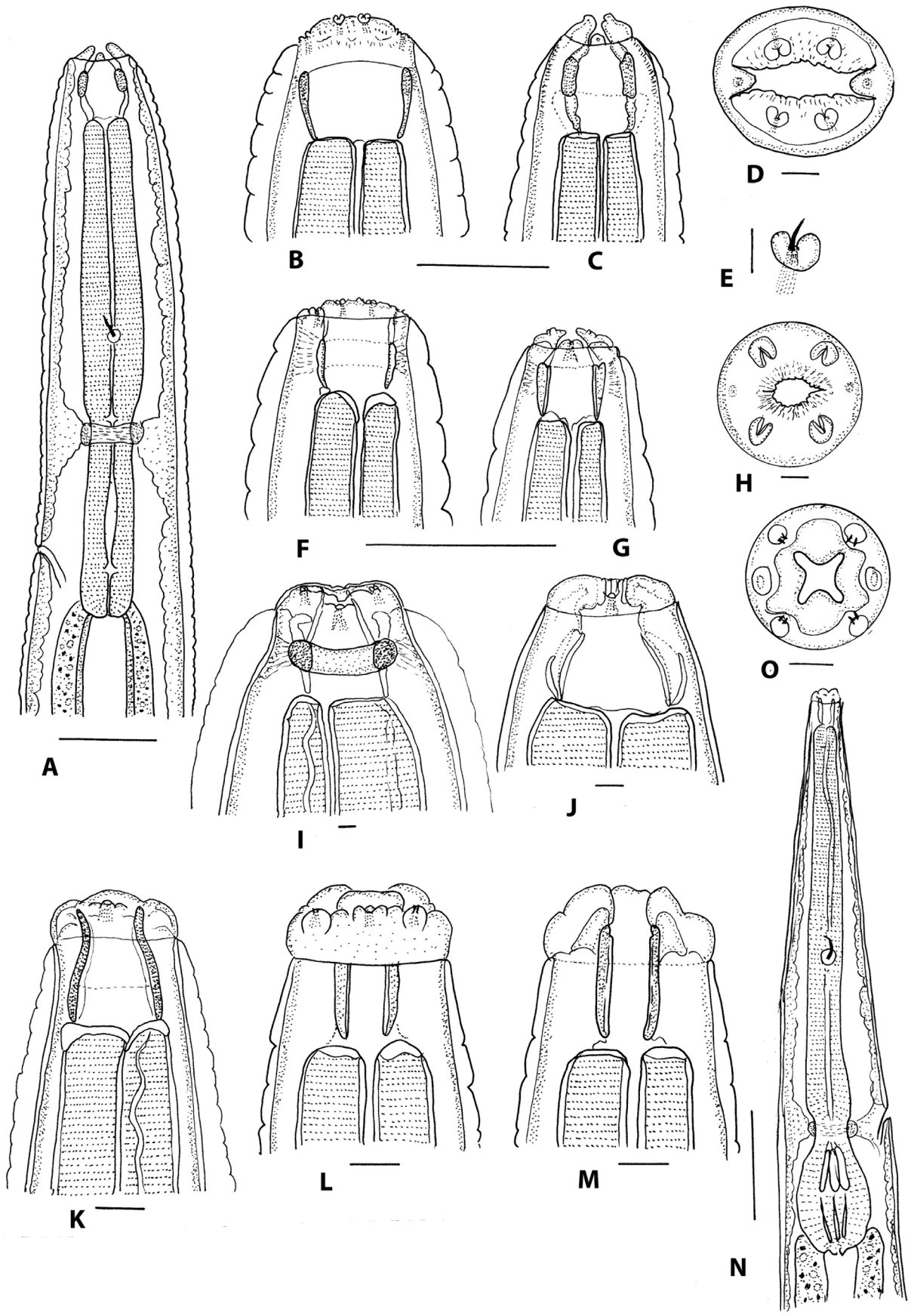
***Thylicostrongylus parvispicularis* (Beveridge, 1983) n.comb.**

Wallabinema parvispiculare Beveridge, 1983, pp. 36–37, figs 115–123 (as *parvispicularis*); Beveridge et al., 1992, p. 365; Griffith et al., 2000, p. 310.

Type data: holotype SAM V2996, allotype SAM V2997,

Fig. 39. Genera *Thylonema* and *Thylicostrongylus n.* gen. A, *Thylonema thylonema*, anterior end, lateral view; B, *Tl. thylonema,* buccal capsule, dorso-ventral view; C, *Tl. thylonema,* buccal capsule, lateral view; D, *Thylonema arundeli,* anterior end, apical view; E, *Tl. thylonema,* amphid; F, *Tl. arundeli*, buccal capsule, dorso-ventral view; G, *Tl. arundeli*, buccal capsule, lateral view; H, *Thylonema barkeri*, anterior end, apical view; I, *Thylonema woodalli*, buccal capsule, lateral view; J, *Tl. barkeri*, buccal capsule, lateral view; K, *Tl. clelandae*, buccal capsule, lateral view; L, *Thylicostrongylus parvispicularis*, buccal capsule, lateral view; M, *Ty. parvispicularis*, optical section through buccal capsule, lateral view, showing cavity surrounding anterior end; N, *Ty. parvispicularis*, anterior end, lateral view; O, *Ty. parvispicularis*, anterior end, apical view. (A–H, J from Beveridge, 1981a; I, K, from Griffith, 1999; L–O from Beveridge, 1983).

Scale-bars: A–C, F, G, N, 0.1 mm; D, E, H–M, O 0.01 mm.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paratypes SAM V2998–3003, BMNH 1981.3690–3691, USNPC 76632.
Type locality: Mission Beach, Qld (17° 58′S 146° 06′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Other hosts: *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: eastern Qld.
Diagnostic features (Figs 39 L–O): Males 3.2–5.4 mm; females 3.8–5.1 mm; cephalic collar present; cephalic papillae domed with paired, tiny setae; 4 flap-like lips, dorsal, ventral and 2 lateral, without pulp cavity; buccal capsule cylindrical, slightly long than wide; oesophageal corpus about 5 times as long as bulb; nerve ring at level of oesophageal isthmus; spicules 0.21–0.29 mm; spicule tip simple; spicule ala diminishes in width towards spicule tip; female tail 0.27–0.36 mm; ovejector J-shaped.

***Thylicostrongylus tasmaniensis* (Beveridge, 1983) n. comb.**

Wallabinema tasmaniense Beveridge, 1983, pp. 39–40, figs 132–139 (as *tasmaniensis*).
Type data: holotype SAM V2986, allotype SAM V2987, paratypes SAM V2988–2995, BMNH 1981.3688–3689, USNPC 76631.
Type locality: Golconda, Tas (41° 10′S 147° 08′E).
Type host: *Thylogale billardierii* (Desmarest, 1822).
Site in host: stomach.
Distribution: Tas.
Representative DNA sequence data: ITS1, 2: MG865651.
Diagnostic features: Males 2.8–3.4 mm; females 2.9–3.8 mm; cephalic collar present; cephalic papillae domed with paired, tiny setae; 4 flap-like lips, dorsal, ventral and 2 lateral, without pulp cavity; buccal capsule cylindrical, slightly long than wide; oesophageal corpus about 5 times as long as bulb; nerve ring at level of oesophageal isthmus; spicules 0.52–0.58 mm; spicule tip simple; spicule ala diminishes in width towards spicule tip; genital cone with enlarged dorsal appendages; female tail 0.27–0.30 mm; ovejector J-shaped.

***Thylicostrongylus thylogale* (Beveridge, 1983) n. comb.**

Wallabinema thylogale Beveridge, 1983, pp. 38–39, figs 124–131, 223; Begg et al., 1995, p. 47; Griffith et al., 2000, p. 310.
Type data: holotype SAM V3004, allotype SAM V3005, paratypes SAM V3006–3008, SAM AHC 11372, BMNH 1981.3692–3697, USNPC 76633.
Type locality: Emu Vale, Qld (28° 14′S 152° 15′E).
Type host: *Thylogale thetis* (Lesson, 1827).
Other hosts: *Thylogale stigmatica* (Gould, 1860); *Petrogale persephone* Maynes, 1982.
Distribution: north-eastern NSW; eastern Qld.
Diagnostic features: Males 2.6–3.4 mm; females 3.2–3.8 mm; cephalic collar present; cephalic papillae domed with single, tiny tri-lobed seta; 4 flap-like lips, dorsal, ventral and 2 lateral, without pulp cavity; buccal capsule cylindrical, slightly long than wide; oesophageal corpus about 5 times as long as bulb; nerve ring at level of oesophageal isthmus; spicules 0.75–0.89 mm; spicule tip simple; spicule ala diminishes in width towards spicule tip; female tail 0.22–0.27 mm; ovejector J-shaped.

Thylonema Beveridge, 1981

Type species: *Tl. thylonema* Beveridge, 1981.
Other species: *Tl. arundeli* Beveridge, 1981; *Tl. barkeri* Beveridge, 1981; *Tl. clelandae* Griffith, 1999; *Tl. woodalli* Griffith, 1999. . . . . .

Generic definition: cephalic collar present; cephalic papillae bilobed with single, central seta; mouth opening circular or laterally elongate; small, lip-like structures present or absent; buccal capsule poorly sclerotized, with or without annulus, without transverse striations; oesophagus short, with distinct isthmus; bulb pyriform or cylindrical, without sclerotised plates; nerve ring surrounds oesophageal isthmus; excretory pore in posterior oesophageal region; deirid in anterior oesophageal region; bursa without sclerotized bosses; spicules elongate, alate, gubernaculum absent; ovejector J-shaped.
Comments: This genus was placed in the tribe Coronostrongylinea by Beveridge (1986d). However, molecular data (Beveridge et al., 2020) suggest a close relationship with the Zoniolaiminea in spite of the lack of supporting morphological data. The genus is readily recognisable by the shape of the cephalic papillae in apical views. It is restricted to species of *Thylogale* in Queensland and Papua New Guinea.

Key to species of Thylonema

1a. Buccal capsule with a prominent annulus in lateral view (Figs 39 B, C, I) 2
1b. Buccal capsule without a prominent annulus in lateral view (Figs 39 F, J) 3

2a. Annulus at anterior extremity of buccal capsule (Fig. 39 C) . . . . . *Tl. thylonema*
2b. Annulus in mid-region of buccal capsule (Fig. 39 I) . . . . . *Tl. woodalli*

3a. Buccal capsule wall thicker anteriorly (Fig. 39 G); without lips . . . . . *Tl. arundeli*
3b. Buccal capsule wall not thicker anteriorly (Figs 39 J, K); with tiny lips 4

4a. Buccal capsule wider than long (Fig. 39 G) . . . . . *Tl. barkeri*
4b. Buccal capsule longer than wide (Fig. 39 K) . . . . . *Tl. clelandae*

***Thylonema arundeli* Beveridge, 1981**

Thylonema arundeli Beveridge, 1981a, pp. 103–105, figs 12–18; Beveridge et al., 1992, p. 364; Griffith et al. 2000, p.310.
Type data: holotype SAM V2042, allotype SAM V2043, paratypes SAM V2044–2055, BMNH 1980.91–92, USNPC 75753.
Type locality: El Arish, Qld (17° 49′S 146° 0′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Site in host: stomach.
Distribution: north-eastern Qld; PNG.
Diagnostic features (Figs 39 D, F): Males 2.6–4.2 mm; females 2.6–4.6 mm; mouth opening and buccal capsule laterally elongate; amphids on separate projections of cephalic collar; lips absent; buccal capsule widest anteriorly, without annulus; spicules 1.22–1.48 mm; ovejector J-shaped.

***Thylonema barkeri* Beveridge, 1981**

Thylogale barkeri Beveridge, 1981a, pp. 105–106, figs 19–26; Beveridge et al., 1992, p. 364; Begg et al., 1995, p. 47; Griffith et al., 2000, p. 310; Spratt & Beveridge, 2016, pp.161, 164.
Type data: holotype SAM V1982, allotype SAM V1983, paratypes SAM V1984–1993, BMNH 1980.97–98, USNPC 75756.
Type locality: Mission Beach, Qld (17° 52′S 146° 06′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Other hosts: *Petrogale persephone* Maynes, 1982; *Thylogale calabyi* Flannery, 1992; *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: eastern Qld; PNG.
Representative DNA sequence data: ITS1, 2: MG865648–9.
Diagnostic features (Figs 39 H, J): Males 4.7–5.8 mm; females 5.6–6.2 mm; amphids not on separate projections of cephalic collar; mouth opening circular with numerous tiny lips; buccal capsule wider than long, outer margin sclerotized only at base; spicules 1.48–1. 70 mm; ovejector J-shaped.

***Thylonema clelandae* Griffith, 1999**

Thylonema clelandae Griffith, 1999, pp. 55–57, figs 9–14; Griffith et al., 2000, p.310.
Type data: holotype SAM AHC 31296, allotype SAM AHC 31297, paratypes SAM AHC 31298.
Type locality: Green Mountain, Lamington National Park, Qld (28° 12′S 153° 05′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Site in host: stomach.
Distribution: south-eastern Qld.
Diagnostic features (Fig. 39 K): Males 4.5–4.8 mm; females 5.05–5.39 mm; amphids not on separate projections of cephalic collar; mouth opening circular with numerous tiny lips; buccal capsule longer than wide, conical, wider posteriorly; sclerotized wall thin, extending full length of capsule; spicules 1.53–1.68 mm; ovejector J-shaped.

***Thylonema thylonema* Beveridge, 1981**

Thylonema thylonema Beveridge, 1981a, pp. 101–103, figs 1–11, 27; Beveridge et al., 1992, p. 364; Griffith et al., 2000, p.310.
Type data: holotype SAM V2034, allotype SAM V2035, paratypes SAM V2036–2041, BMNH 1980.89–90.
Type locality: Mission Beach, Qld (17° 52′S 146° 06′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Site in host: stomach.
Distribution: north-eastern Qld.
Representative DNA sequence data: ITS1, 2: MG865650.
Diagnostic features (Figs 39 A–C, E, 45 I): Males 4.8–5.9 mm; females 6.0–8.0 mm; mouth opening and buccal capsule laterally elongate; amphids on separate projections of cephalic collar; lips absent; buccal capsule with annulus at anterior extremity; spicules 1.91–2.02 mm; ovejector J-shaped.

***Thylonema woodalli* Griffith, 1999**

Thylonema woodalli Griffith, 1999, pp. 53–55, figs 1–8; Griffith et al., 2000, p. 310.
Type data: holotype SAM AHC 31299, allotype SAM AHC 31300, paratypes SAM AHC 31301.
Type locality: Mount Glorious, Qld (27° 19′S 152° 46′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Other hosts: *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: south-eastern Qld.

Diagnostic features (Fig. 39 I): Males 5.04–7.90 mm; females 8.08–9.70 mm; mouth opening and buccal capsule laterally elongate; amphids not on separate projections of cephalic collar; lips absent; buccal capsule with annulus in mid–region; spicules 1.7–2.2 mm; ovejector J-shaped.

Thylostrongylus Beveridge, 1982

Type species: *Ts. parvus* Beveridge, 1982.
Other species: *Ts. tasmaniensis* Beveridge, 1982; *Ts. franklinae* Griffith, 1999.
Generic definition: cephalic collar present; labial collar with labial crown of 8 petaloid elements; cephalic papillae dome-shaped with one or two short setae; buccal capsule heavily sclerotized, circular in cross section with or without prominent transverse striations; oesophagus with slender corpus, distinct isthmus and ovoid bulb lined with 3 pairs of sclerotized plates; deirid in oesophageal region anterior to nerve ring; nerve ring in mid-oesophageal region or anterior to oesophageal bulb; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum absent; genital cone with prominent appendages; vulva immediately anterior to anus; ovejector J-shaped.

Comments: The genus as currently defined includes three species united by the possession of a labial crown and an oesophageal bulb lined with sclerotized plates. Apart from these features, *Ts. parvus* differs significantly in buccal and oesophageal morphology from the remaining two species and therefore *Thylostrongylus*, as currently defined, may represent two genera. The genus is found only in species of pademelons (*Thylogale* spp.).

Key to species of Thylostrongylus

1a. Buccal capsule 4 times longer than wide (Fig. 40 B) . . . . . *Ts. parvus*
1b. Buccal capsule twice as long as wide (Fig. 40 E) 2

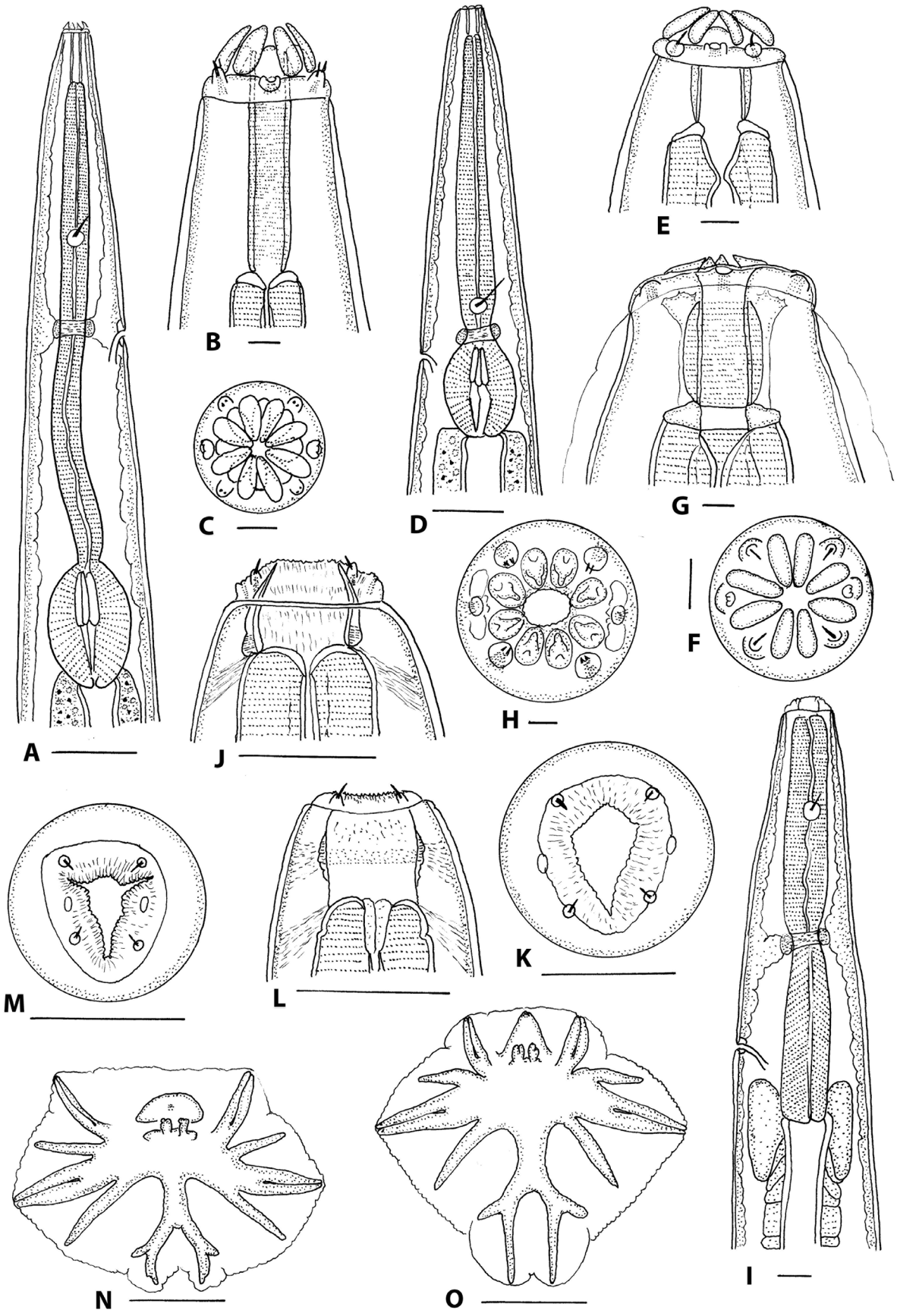
2a. Buccal capsule with prominent transverse striations (Fig. 40 G); spicules 1.82–1.94 mm . . . . . *Ts. franklinae*
2b. Buccal capsule without prominent transverse striations (Fig. 40 E); spicules 1.40–1.72 mm . . . . . *Ts. tasmaniensis*

Thylostrongylus franklinae Griffith, 1999

Thylostrongylus franklinae Griffith, 1999, pp. 57–59; Griffith et al., 2000, p. 310.
Type data: holotype SAM AHC 31307, allotype SAM AHC 31308, paratypes SAM AHC 31309.
Type locality: Green Mountain, Lamington National Park, Qld (28° 10′S 152° 59′E).
Type host: *Thylogale stigmatica* (Gould, 1860).
Other hosts: *Thylogale thetis* (Lesson, 1827).
Site in host: stomach.
Distribution: south-eastern Qld.
Diagnostic features (Figs 40 G, H): Males 6.4–6.6 mm, females 6.3–7.5 mm; labial crown with 8 petaloid elements; cephalic papillae with short, paired setae; buccal capsule short, cylindrical with prominent transverse striations; oesophageal corpus short; nerve ring and deirid at level of oesophageal isthmus; excretory pore at level of oesophageal bulb; spicules 1.82–1.94 mm; ovejector J-shaped.
Comments: This species is known only from two species of pademelons (*Thylogale* spp.) from south-eastern Queensland.

Fig. 40. Genera *Thylostrongylus*, *Trigonostonema*. A, *Thylostrongylus parvus*, anterior end, lateral view; B, *Ts. parvus,* buccal capsule, lateral view; C, *Ts. parvus*, anterior end, apical view; D, *Thylostrongylus tasmaniensis*, anterior end, lateral view; E, *Ts. tasmaniensis*, buccal capsule, lateral view; F, *Ts. tasmaniensis*, anterior end, apical view; G, *Thylostrongylus franklinae*, buccal capsule, lateral view; H, *Ts. franklinae*, anterior end, apical view; I, *Trigonostoma trigonostoma*, anterior end, lateral view; J, *Tr. trigonostoma,* buccal capsule, lateral view; K, *Tr. trigonostoma,* anterior end, apical view; L, *Trigonostonema longibursatum*, buccal capsule, lateral view; M, *Tr. longibursatum,* anterior end, apical view; N, *Tr. trigonostoma,* bursa, apical view; O, *Tr. longibursatum,* bursa, apical view. (A–F from Beveridge, 1982; G, H, from Griffith, 1999; I–O from Beveridge, 1981b).

Scale-bars: A, D, I, J–O, 0.1 mm; B–C, E–H, 0.01 mm.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***Thylostrongylus parvus* Beveridge, 1982**

Thylostrongylus parvus Beveridge, 1982, pp. 51–53, figs 167–174; Griffith et al., 2000, p. 310.

Type data: holotype SAM V1804, allotype SAM V1805, paratypes SAM V1806–1815, BMNH 1979. 889–892, USNPC 75316.

Type locality: Emu Vale, Qld (28° 14′S 152° 15′E).

Type host: *Thylogale thetis* (Lesson, 1827).

Other hosts: *Thylogale stigmatica* (Gould, 1860).

Site in host: stomach.

Distribution: eastern Qld, north-eastern NSW.

Diagnostic features (Figs 40 A–C): Males 3.3–4.2 mm, females 4.1–5.8 mm; labial crown with 8 petaloid elements; cephalic papillae with short, paired setae; buccal capsule elongate, cylindrical with prominent transverse striations; oesophageal corpus elongate; nerve ring in mid-oesophageal region; excretory pore at level of nerve ring; deirid anterior to nerve ring; bursa without sclerotized bosses; spicules 1.00–1.12 mm; ovejector J-shaped.

Comments: This distinctive species is readily separable from congeners by its elongate buccal capsule. It appears to be restricted to south-eastern Queensland and north-eastern New South Wales (Beveridge, 1982; Griffith et al., 2000).

***Thylostrongylus tasmaniensis* Beveridge, 1982**

Thylostrongylus tasmaniensis Beveridge, 1982, pp. 53–54, figs 175–182; Griffith et al., 2000, p. 310.

Type data: holotype SAM V2161, allotype SAM V2162, paratypes SAM V2163–2166, BMNH 1980.605, USNPC 75879.

Type locality: Golconda, Tas. (41° 10′S 147° 18′E).

Type host: *Thylogale billardierii* (Desmarest, 1822).

Other hosts: *Thylogale stigmatica* (Gould, 1860); *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: south-eastern Qld, Tas.

Representative DNA sequence data: ITS1, 2: MG865651.

Diagnostic features (Figs 40 D–F): Males 3.1–4.9 mm; females 3.6–5.5 mm; labial crown with 8 petaloid elements; cephalic papillae with short, single seta; buccal capsule short, cylindrical without prominent transverse striations; oesophageal corpus short; nerve ring and deirid at level of oesophageal isthmus; excretory pore at level of oesophageal bulb; spicules 1.40–1.72 mm; ovejector J-shaped.

Comments: This species was originally described from *Thyl. billardierii* in Tasmania (Beveridge, 1982), but was subsequently found in two additional species of *Thylogale* in south-eastern Queensland (Griffith et al., 2000). The current distribution of this species is highly disjunct, but this may reflect the lack of sampling of *Thylogale* spp. in New South Wales.

Trigonostonema Beveridge, 1981

Type species: *Tr. trigonostoma* Beveridge, 1981. . . .

Other species: *Tr. longibursatum* Beveridge, 1981. . .

Generic definition: cephalic collar present; labial crown present composed of numerous tiny elements; submedian papillae conical with single seta; mouth opening dorso-ventrally elongate, triangular to trapezoidal; buccal capsule as wide as or wider than long, poorly sclerotized, without transverse striations, with annulus either in middle or at posterior end; lining longitudinally striated; prominent radial musculature supporting oesophago-intestinal junction; oesophageal corpus elongate; isthmus indistinct; bulb cylindrical, slightly shorter than corpus; anterior intestinal cells enlarged, surrounding base of oesophageal bulb; nerve ring surrounds oesophageal isthmus; deirid in anterior oesophageal region; excretory pore near oesophago-intestinal junction; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum absent; ovejector J-shaped.

Comments: Beveridge (1981b) described a “leaf crown” of numerous elements surrounding the mouth opening. Scanning electron micrographs of both known species (Beveridge, 1981b, figs 24, 25) show that the ‘leaf crown” elements arise from the labial region and it is therefore described here as a labial crown. The genus is known only from pademelons (*Thylogale* spp.) from Queensland and Papua New Guinea.

Key to species of Trigonostonema

1a. Annulus surrounding base of buccal capsule (Fig. 40 J); spicules 0.93–1.30 mm; dorsal lobe of bursa not longer than lateral lobes (Fig. 40 N); female tail 0.38–0.44 mm . . . . . *Tr. trigonostoma*

1b. Annulus in middle of buccal capsule (Fig. 40 L); spicules 0.67–0.90 mm; dorsal lobe of bursa longer than lateral lobes (Fig. 40 O); female tail 0.32–0.39 mm . . . . . *Tr. longibursatum*

***Trigonostonema longibursatum* Beveridge, 1981 .**

Trigonostonema longibursatum Beveridge, 1981b, pp. 95–96, figs 12–23, 25 (as *longibursata*); Beveridge et al., 1992, p. 365; Griffith et al., 2000, p. 310; Spratt & Beveridge, 2016, p. 160.

Type data: holotype SAM V2059, allotype SAM V2060, paratypes SAM V2061–2065, BMNH 1980.95–96, US-NPC 75755.

Type locality: Tolga, Qld (17° 13′S 145° 29′E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Thylogale browni* (Ramsay, 1877); *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: eastern Qld, PNG.

Diagnostic features (Figs 40 L, M): Males 4.9–6.2 mm; females 5.9–8.3 mm; buccal capsule as wide as long; annulus surrounding mid-region of buccal capsule; spicules 0.69–0.90 mm; dorsal lobe of bursa longer than lateral lobes; female tail 0.32–0.39 mm; ovejector J-shaped.

***Trigonostonema trigonostoma* Beveridge, 1981**

Trigonostonema trigonostoma Beveridge, 1981b, pp. 94–95, figs 1–11, 24; Beveridge et al., 1992, p. 365; Griffith et al., 2000, p. 310; Spratt & Beveridge, 2016, p. 161.

Type data: holotype SAM V2056, allotype SAM V2057, paratype SAM V2058.

Type locality: Mission Beach, Qld (17° 58′S 146° 06′).

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Thylogale calabyi* Flannery, 1992; *Thylogale thetis* (Lesson, 1827).

Site in host: stomach.

Distribution: eastern Qld, PNG.

Representative DNA sequence data: ITS1, 2: MG865652.

Diagnostic features (Figs 40 I–K): Males 4.3–7.2 mm; females 7.6–9.8 mm; buccal capsule wider than long; annulus surrounding base of buccal capsule; spicules 0.93–1.30 mm; dorsal lobe of bursa not longer than lateral lobes; female tail 0.38–0.44 mm; ovejector J-shaped.

Wallabinema Beveridge, 1983

Type species: *Wallabinema australe* (Johnston & Mawson, 1939).

Other species: *W. cobbi* (Kung, 1948); *W. labiatum* (Johnston & Mawson, 1939); *W. petrogale* Beveridge, 2020.

Generic definition: Cephalic collar present; cephalic papillae domed, armed with single seta; mouth opening circular or elongate, with 4 flap-like or bulbous lips with or without pulp cavities, in dorsal, ventral and lateral positions; interlabia absent; buccal capsule cylindrical, moderately sclerotized, lacking transverse striations; oesophagus elongate without accessory fusiform bulb in mid-oesophageal region; terminal bulb ovoid, lined with 3 pairs of elongate sclerotized plates; nerve ring in anterior oesophageal region; excretory pore and deirids at level of nerve ring; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum absent; ovejector J-shaped.

Comments: This genus contains several distinct morphological groups and molecular data (Chilton et al., 2018, fig.1; Beveridge et al., 2020, fig. 5) suggest the presence of three separate clades: 1, *W. australe* and *W. cobbi*, 2, *W. labiatum* and 3, *W. tasmaniense* and *W. macropodis*. These three clades are also reflected in morphological differences between the three groups of species involving the relative length of the oesophagus, the position of the nerve ring (anterior or encircling the oesophageal isthmus) and the lips. Based on their morphological uniformity (short oesophagus; nerve ring immediately anterior to the oesophagesl bulb), *W. gallardi*, *W. macropodis*, *W. parvispiculare*, *W. tasmaniense* and *W. thylogale* have been removed to a new genus, *Thylicostrongylus*. The position of *W. labiatum* is currently unclear as it has an oesophagus resembling that of *Thylicostrongylus* n. gen., but the nerve ring is in the anterior oesophageal region. It has been left within *Wallabinema* pending the availability of additional morphological and molecular data. Several of the new combinations made by Beveridge (1983) (as *W. australis*, *W. labiatus*) were incorrectly given masculine endings; the genus is neuter and the endings were subsequently corrected (Spratt & Beveridge, 2016).

Key to species of Wallabinema

1a. Lips prominent, bulbous; buccal capsule walls sinuous; buccal capsule dorso–ventrally elongate (Figs 41 B, C) . . . . . *W. australe*

1b. Lips flap-like, buccal capsule cylindrical, walls parallel (Figs 41 F, E, K) 2

2a. Spicules 2.36–2.66 mm long; buccal capsule slightly longer than wide (Fig. 41 E) . . . *W. cobbi*

2b. Spicules < 1.30 mm long; buccal capsule at least 2.5 times as long as wide (Figs 41 F, K) 3

3a. Oesophagus 0.94–1.15 mm in males, 1.00–1.20 mm in females; spicule tip simple, ala terminates at tip; lips bilobed at tips. . . . . *W. petrogale*

3b. Oesophagus 0.52–0.64 mm in males, 0.61–0.73 mm in females; spicule tip simple; ala terminates anterior to tip; lips not bilobed at tip . . . . *W. labiatum*

***Wallabinema australe* (Johnston & Mawson, 1939)**

Buccostrongylus australis Johnston & Mawson, 1939a, pp. 142–143, figs 60–62; 1939b, p. 527.

Zoniolaimus australis: Kung, 1948, pp. 102, 105, 106; Skrjabin et al., 1952, pp. 163, 784; Popova, 1960, pp. 72–73; Yamaguti, 1961, p. 403.

Wallabinema australe: Beveridge, 1983, pp. 30–32, figs 83–90, 220 (as *australis*); Aussavy et al., 2011, p. 16; Vendl & Beveridge, 2014; p. 108; Spratt et al., 2017, p. 241.

Type data: holotype and allotype SAM V1558.

Type locality: Eidsvold, Qld (25° 22′S 151° 07′E).

Type host: *Thylogale stigmatica* (Gould, 1860).

Other hosts: *Notamacropus dorsalis* (Grey, 1837); *Notamacropus rufogriseus* (Desmarest, 1817); *Thylogale billardierii* (Desmarest, 1822).

Site in host: stomach.

Distribution: Qld, NSW, Vic, Tas.

Representative DNA sequence data: ITS1, 2: MG 865653.

Diagnostic features (Figs 41 A–C): Males 4.1–6.7 mm; females 4.8–7.2 mm; cephalic collar present; cephalic papillae domed with single short seta; 4 flap-like lips, dorsal, ventral and 2 lateral, with pulp cavity; buccal capsule cylindrical, slightly longer than wide; oesophageal corpus about 7 times as long as bulb; nerve ring in mid-oesophageal region; spicules 0.93–1.42 mm; ovejector J-shaped.

Comments: *Wallabinema australe* is a common parasite of *N. rufogriseus* (Beveridge, 1983; Aussavy et al., 2011; Vendl & Beveridge, 2014; Spratt et al., 2017) but occurrences in sympatric host species (*Thyl. stigmatica*, *Thyl. billardierii* and *N. dorsalis*) are based on single collections (Beveridge et al, 1998; Griffith et al., 2000), suggesting that these are accidental hosts.

***Wallabinema cobbi* (Kung, 1948)**

Zoniolaimus cobbi Kung, 1948, pp. 93, 100–102, 107, figs 13–18; Skrjabin et al., 1952, p. 172; Popova, 1960, pp. 73–74, fig. 44; Yamaguti, 1961, p. 403; Mawson, 1964, pp. 241–243, figs 22–25; Mykytowycz, 1964, p. 682; Arundel et al., 1979, p. 365; Beveridge & Arundel, 1979, p. 72.

Wallabinema cobbi: Beveridge, 1983, pp. 32–34, figs 91–102, 221; Beveridge et al., 1998, p. 481; Lott et al., 2014, p. 78; Beveridge, 2020c, p. 4, 2020e, p. 204.

Type data: syntypes BMNH 1949.12.23.56–75.

Type locality: London Zoological Gardens, UK.

Type host: *Notamacropus rufogriseus* (Desmarest, 1817).

Other hosts: *Macropus fuliginosus* (Desmarest, 1817); *Osphranter robustus* (Gould, 1840); *O. rufus* (Desmarest, 1822).

Site in host: stomach.

Distribution: Qld, NSW.

Representative DNA sequence data: ITS1, 2: MG 865654.

Diagnostic features (Figs 41 D, E): Males 5.2–7.2 mm; females 5.8–10.9 mm; cephalic collar present; cephalic papillae domed with single short seta; 4 lips, bilobed at apices, dorsal, ventral and 2 lateral, with pulp cavity; buccal capsule with sinuous walls in lateral view, dorso-ventrally elongated; oesophageal corpus about 5 times as long as bulb; nerve ring in mid-oesophageal region; spicules 2.32–2.66 mm; ovejector J-shaped.

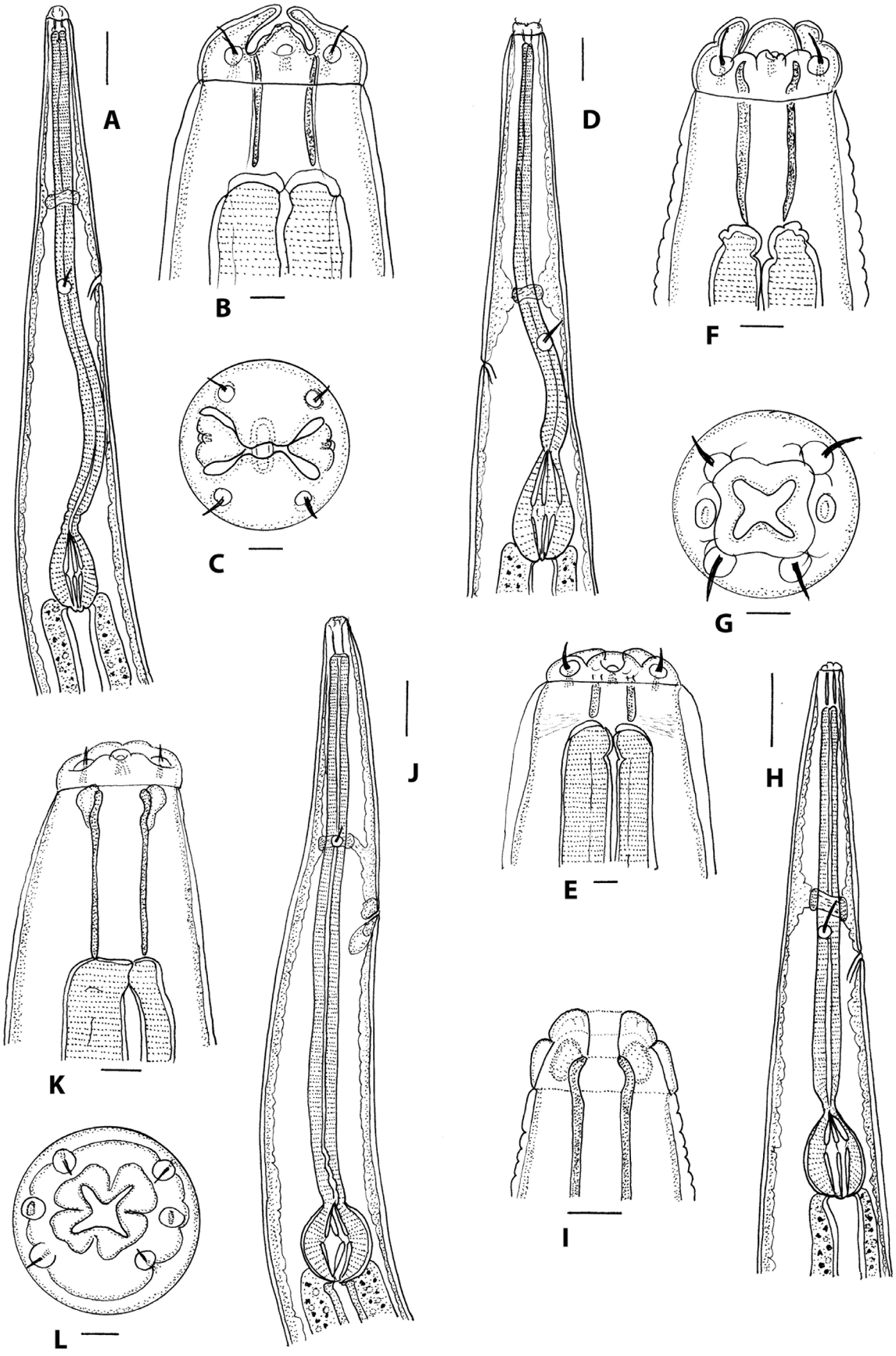
Comments: This species was first described from captive *N. rufogriseus* in England and is still present in zoo populations in that country (Beveridge, 1983). In wild animals, it occurs in large numbers in *O. rufus* (Arundel et al., 1979) and is occasionally found in small numbers in sympatric *Mac. fuliginosus* (Beveridge & Arundel, 1979) and *O. robustus* (Beveridge et al., 1998; Beveridge, 2020c, p. 4). *Osphranter rufus* appears to be the usual host in the wild.

***Wallabinema labiatum* (Johnston & Mawson, 1939)**

Buccostrongylus labiatus Johnston & Mawson, 1939b, p. 527, figs 37–38; 1939d, p. 308; Skrjabin et al., 1952, p. 164; Yamaguti, 1961, p. 404.

Fig. 41. Genus *Wallabinema*. A, *Wallabinema australe*, anterior end, lateral view; B, *Wa. australe*, buccal capsule, lateral view; C, *Wa. australe*, anterior end, apical view; D, *Wallabinema cobbi*, anterior end, lateral view; E, *Wa. cobbi*, buccal capsule, lateral view; F, *Wallabinema labiatum*, buccal capsule, lateral view; G, *Wa. labiatum,* anterior end, apical view; H, *Wa. labiatum,* anterior end, lateral view; I, *Wa. labiatum,* anterior region of buccal capsule showing cavity surrounding anterior end; J, *Wallabinema petrogale*, anterior end, lateral view; K, *Wa. petrogale*, buccal capsule, lateral view; L, *Wa. petrogale,* anterior end, apical view. (A–I from Beveridge, 1983; J–L from Beveridge, 2020b).

Scale-bars: A, D, H, J, 0.1 mm; B, C, E–G, I, K, L, 0.01 mm.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Zoniolaimus labiatus: Kung, 1948, pp. 106–107; Popova, 1960, p. 75, fig. 45.
Wallabinema labiatum: Beveridge, 1983, pp. 34–36, figs 103–114 (as *labiatus*); Beveridge et al., 1989, p. 277; Aussavy et al., 2011, p. 16; Vendl & Beveridge, 2014, p. 108; Beveridge, 2016, p. 210; Spratt et al., 2017, p. 241.
Type data: holotype and allotype, SAM V1371.
Type locality: Bathurst, NSW (33° 25′S 149° 35′E).
Type host: *Notamacropus rufogriseus* (Desmarest, 1817).
Other hosts: *Petrogale penicillata* (Gray, 1827); *Wallabia bicolor* (Desmarest, 1804).
Site in host: stomach.
Distribution: Qld, NSW, Vic, Tas.
Representative DNA sequence data: ITS1, 2: MG 865655.
Diagnostic features (Figs 41 F–I): Males 2.9–4.6 mm; females 3.5–4.9 mm; cephalic collar present; cephalic papillae domed with single short seta; 4 triangular, flap-like lips, dorsal, ventral and 2 lateral, without pulp cavity; buccal capsule cylindrical, 3 times as long as wide; oesophageal corpus about 5 times as long as bulb; nerve ring in mid-oesophageal region; spicules 0.93–1.17 mm; spicule tip slightly bilobed; spicule ala terminates abruptly anterior to spicule tip; female tail 0.40–0.49 mm; ovejector J-shaped.
Comments: The usual host of this parasite is *N. rufogriseus*. Records from *Pet. penicillata* (Beveridge et al., 1989) and *Wal. bicolor* (Beveridge, 1983, 2016) represent incidental occurrences in these host species.

Wallabinema petrogale Beveridge, 2020

Wallabinema petrogale Beveridge, 2020b, pp. 58–60, figs 1–9.
Thylostrongylus sp.: Beveridge et al., 1989, p. 277.
Type data: holotype SAM AHC 48774, allotype SAM AHC 48775, paratypes SAM AHC 11933, BMNH 2019.8.12.24–29.
Type locality: Bonalbo, NSW (28° 44′S 152° 37′E).
Type host: *Petrogale penicillata* (Gray, 1827).
Other hosts: *Petrogale inornata* Gould, 1842.
Site in host: stomach.
Distribution: north-eastern NSW, eastern Qld.
Diagnostic features (Figs 41 J–L): Males 4.1–5.9 mm; females 5.1–6.1 mm; cephalic collar present; cephalic papillae domed with single seta; 4 flap-like lips, dorsal, ventral and 2 lateral, without pulp cavity; lips divided at base; buccal capsule cylindrical, 2.5 times as long as wide; oesophageal corpus about 5 times as long as bulb; nerve ring in mid-oesophageal region; spicules 1.12–1.27 mm; spicule tip simple; spicule ala diminishes in width towards spicule tip; female tail 0.24–0.33 mm; ovejector J-shaped.

Woodwardostrongylus Wahid, 1964

Type species: *Wo. woodwardi* (Wood, 1931).
Other species: *Wo. obendorfi* Mawson, 1976; *Wo. petrogale* Beveridge, 1998.

Generic definition: cephalic and labial collars absent; mouth opening tiny, circular, with row of denticles on each side; buccal capsule dorso-ventrally elongate, prominently striated; oesophagus elongate, claviform; nerve ring in mid-oesophageal region; deirid and excretory pore at same level in posterior oesophageal region; bursa without sclerotised bosses; dorsal ray divided to base; spicules elongate, alate; gubernaculum present; female tail conical; ovejector Y-shaped.
Comments: Species of this genus are usually found with the anterior end embedded in the gastric or oesophageal mucosa.

Key to species of Woodwardostrongylus

1a. Mouth opening with 16 pairs of denticles . . . . . *Wo. woodwardi*
1b. Mouth opening with 6 pairs of denticles . . . . . .*Wo. obendorfi*
1c. Mouth opening with 4 pairs of denticles . . . . . .*Wo. petrogale*

Woodwardostrongylus obendorfi Mawson, 1976

Woodwardostrongylus obendorfi Mawson, 1976, pp. 121–123, figs 1–11; Durette–Desset & Beveridge, 1980, pp. 77–79, fig. 1; Beveridge et al., 1989, p. 277; Spratt et al., 2017, p. 242.
Type data: "types", SAM V6387.
Type locality: Rivertree, NSW (28° 39′S 152° 18′E) (incorrectly given as Dorrigo, NSW in Mawson, 1976).
Type host: *Notamacropus parryi* (Bennett, 1853).
Other hosts: *Notamacropus agilis* (Gould, 1842); *Notamacropus rufogriseus* (Desmarest, 1817); *Osphranter robustus* (Gould, 1840); *Petrogale assimilis* Ramsay, 1877; *Petrogale godmani* Thomas, 1923; *Petrogale herberti* Thomas, 1926; *Petrogale inornata* Gould, 1842; *Petrogale mareeba* Eldridge & Close, 1992; *Petrogale penicillata* (Gray, 1827); *Petrogale sharmani* Eldridge & Close, 1992; *Wallabia bicolor* (Desmarest, 1804).
Site in host: stomach and oesophagus.
Distribution: Qld, NSW, PNG.
Representative DNA sequence data: ITS1, 2: MG865657.
Diagnostic features (Fig. 42 H): Males 15.9–16.7 mm; females 24–26 mm; mouth opening with 6 pairs of

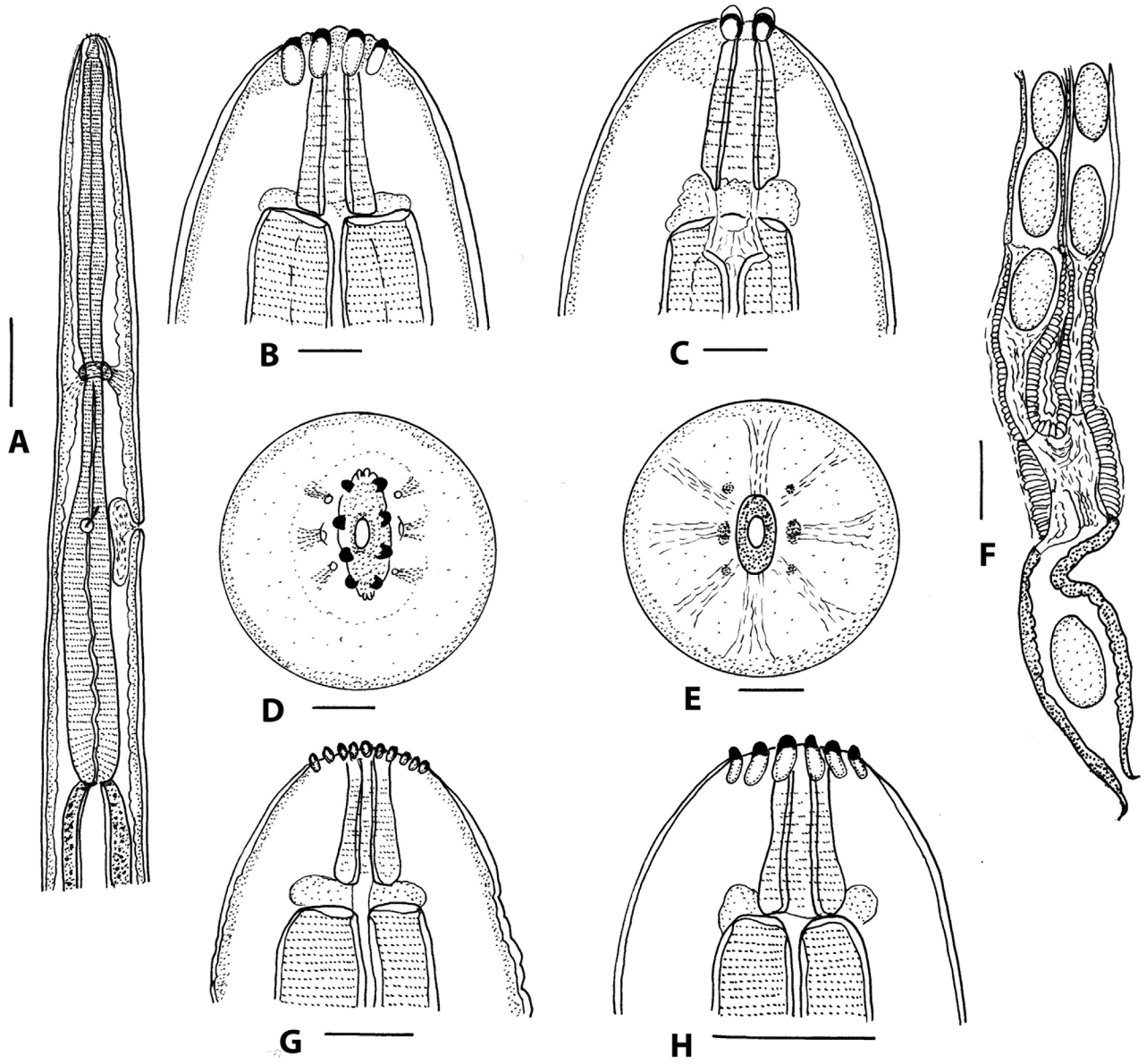


Fig. 42. Genus *Woodwardostrongylus*. A, *Woodwardostrongylus petrogale*, anterior end, lateral view; B, *Wo. petrogale,* anterior end, lateral view; C, *Wo. petrogale,* anterior end, dorso-ventral view; D, *Wo. petrogale,* anterior end, apical view; E, *Wo. petrogale,* anterior end, transverse optical section through buccal capsule; F, *Wo. petrogale,* vagina and ovejector; G, *Woodwardostrongylus woodwardi*, anterior end, lateral view; H, *Woodwardostrongylus obendorfi*, anterior end, lateral view. (A–F from Beveridge, 1998b; G, from Mawson, 1971; H, from Mawson, 1976).

Scale-bars: A, F, 0.1 mm; B–E, G, H, 0.01 mm.

denticles; spicules 1.70–2.10 mm; female tail 0.18–0.22 mm long; vagina 0.8 mm long; ovejector Y-shaped.
Comments: The type locality given by Mawson (1976) is an error and was Rivertree rather than Dorrigo in New South Wales. The type material was collected on a joint collecting trip with one of the current authors and P.M. Mawson. Other macropodids were collected at Dorrigo, but *N. parryi* was only collected at Rivertree. The report of this nematode from *Pet. lateralis* in Spratt & Beveridge (2016) is an error and refers to *Wo. woodwardi*.

***Woodwardostrongylus petrogal*e Beveridge 1998**
*Woodwardostrongylus petrogal*e Beveridge 1998b, p.74, figs 1–12.
Type data: holotype SAM AHC 30592, allotype SAM AHC 30593, paratypes SAM AHC 13790.
Type locality: Arnhem Land, NT.
Type host: *Petrogale concinna* Gould.
Other hosts: *Petrogale wilkinsi* Thomas, 1926 (as *Petrogale brachyotis* (Gould, 1841)).
Site in host: stomach.
Distribution: NT (Arnhem Land).
Diagnostic features (Figs 42 A–F): Males 13.1–15.5 mm; females 16.4–22.8 mm; mouth opening with 4 pairs of denticles; spicules 0.90–1.07 mm; female tail 0.11–0.17 mm; vagina 0.31–0.48 mm long; ovejector Y-shaped.
Comments: The ovejector illustrated by Beveridge (1987, fig. 3 I) as "*Woodwardostrongylus* undescribed" is that of *Wo. petrogale*.

***Woodwardostrongylus woodwardi* (Wood, 1931)**
Pharyngostrongylus woodwardi Wood, 1931, pp. 213–215, figs 4–6.
Woodwardostrongylus woodwardi: Wahid, 1964, pp. 184–185, figs 7–11.
Cristaceps woodwardi: Mawson, 1971, pp. 174–175, figs 16–19.
Type data: not known.
Type locality: Kimberley Division, Western Australia.
Type host: *Osphranter robustus woodwardi* Thomas, 1922.
Other hosts: *Petrogale lateralis pearsoni* Thomas, 1922.
Site in host: stomach.
Distribution: WA (Kimberley Division); SA (west coast).
Diagnostic features (Fig. 42 G): Males 15–17 mm; females 30–39 mm; mouth opening dorso-ventrally elongate with 16 pairs of denticles; spicules 1.4 mm; female tail 0.22–0.23 mm; vagina 0.7–1.0 mm; ovejector Y-shaped.
Comments: This species has been described from two different host species from very different geographical localities and warrants redescription. Mawson (1971) gave the type host as *Osphranter* (= *Macropus*) *bernardus*, but it is in fact *O. robustus woodwardi*. The description of this species remains incomplete.

Zoniolaimus Cobb, 1898

Type species: *Zoniolaimus setifera* Cobb, 1898.
Other species: *Z. buccalis* (Johnston & Mawson, 1939); *Z. dendrolagi* Beveridge, 1983; *Z. elegans* Beveridge, 1983; *Z. latebrosus* Huby-Chilton, Beveridge, Gasser & Chilton, 2002; *Z. mawsonae* Beveridge, 1983; *Z. niuginiensis* Beveridge, 1983; *Z. occidentalis* Beveridge, 1983; *Z. petrogale* Beveridge, 1983.

Generic definition: cephalic collar absent (in type and other species) or present; cephalic papillae domed, armed with single, elongate seta; mouth opening circular or quadrangular, with 4 lips,either simple and flap-like or ornamented anteriorly, without pulp cavities, in submedian positions; interlabia present or absent; buccal capsule cylindrical or campanulate, moderately sclerotized, lacking transverse striations or with very faint transverse striations; oesophagus elongate with accessory fusiform bulbin mid-oesophageal region; terminal bulb ovoid, lined with 3 pairs of elongate sclerotized plates; nerve ring in anterior oesophageal region; excretory pore and deirids at level of nerve ring; bursa without sclerotized bosses; spicules elongate, alate; gubernaculum present or absent; ovejector J-shaped.
Comments: This genus is immediately recognisable with its elongate oesophagus and accessory fusiform bulb in the mid-oesophageal region.

Key to species of Zoniolaimus

1a. Lips and interlabia ornately sculptured anteriorly (Figs 43, M, O) 8
1b. Lips not ornately sculptured anteriorly 2

2a. Buccal capsule walls sinuous in lateral view (Fig. 43 H) . . . . . *Z. occidentalis*
2b. Buccal capsule walls not sinuous in lateral view . 3

3a. Buccal capsule 2–3 times as long as wide (Fig. 43 F) . . . . . *Z. petrogale*
3b. Buccal capsule only slightly longer than wide . . 4

4a. Spicule length > 2.2 mm . . . . . *Z. elegans*
4b. Spicule length < 2.2 mm 5

5a. Spicule length > 1.5 mm 6
5b. Spicule length < 1.40 mm 7

6a. Lateral interlabia present (Fig. 43 Q); female tail 0.32–0.42 mm long . . . . *Z. buccalis*
6b. Lateral, dorsal and ventral interlabia present (Fig. 43 E); female tail 0.65–0.78 mm long . . . . . *Z. latebrosus*

7a. Dorsal lip of genital cone with numerous appendages; female tail 0.52–0.68 mm . . . . . *Z. mawsonae*
7b. Dorsal lip of genital cone without numerous appendages; female tail 0.40–0.53 mm . . . . . *Z. setifera*

8a. Spicules 2.00–2.25 mm; cephalic setae long (Fig. 43 M) . . . . . *Z. dendrolagi*
8b. Spicules 1.70–1.95 mm; cephalic setae short (Fig. 43 O) . . . . . *Z. niuginiensis*

***Zoniolaimus buccalis* (Johnston & Mawson, 1939)**

Buccostrongylus buccalis Johnston & Mawson, 1939a, pp. 141–142, figs 56–59; 1939b, p. 527; 1939d, p. 307; 1940a, p. 468; Skrjabin et al., 1952, p. 162; Yamaguti, 1961, p. 404.

Zoniolaimus buccalis: Kung, 1948, pp. 105–106; Skrjabin et al., 1952, p. 784; Popova, 1960, p. 73; Beveridge, 1983, pp. 19–21, figs 18–26, 219; Beveridge et al., 1989, p. 481; Turni & Smales, 2001, p. 406.

Type data: syntypes SAM V1557.
Type locality: Upper Burnett River, Qld (24° 45′S 152° 23′E).
Type host: *Notamacropus dorsalis* (Gray, 1837).
Other hosts: *Notamacropus parma* (Waterhouse, 1846); *Onychogalea fraenata* (Gould, 1840).
Site in host: stomach.
Distribution: Qld, NSW.
Representative DNA sequence data: ITS1, 2: MG 865658.
Diagnostic features (Fig. 43 Q): Males 5.5–6.7 mm; females 5.8–7.2 mm; lips flap-like, inornate; lateral interlabia absent; cephalic setae elongate; buccal capsule unstriated; flap-like valves present at base of buccal capsule; spicules 1.51–1.75 mm; gubernaculum absent; female tail elongate, 0.32–0.42 mm long; ovejector J-shaped.
Comments: This species is common in *N. dorsalis* (see Beveridge et al., 1998), while records from other host species are limited.

***Zoniolaimus dendrolagi* Beveridge, 1983**

Zoniolaimus dendrolagi Beveridge, 1983, pp. 24–26, figs 48–59; Beveridge et al., 1992, p. 365; Shima et al., 2019, p. 62.

Type data: holotype, SAM V2957, allotype SAM V2958, paratypes SAM V2959–2968, BMNH 1981.3680–3681, USNPC 76627.
Type locality: Atherton, Qld (17° 16′S 145° 29′E).
Type host: *Dendrolagus lumholtzi* Collett, 1884.
Site in host: stomach.
Distribution: north-eastern Qld.
Representative DNA sequence data: ITS1, 2: MG 865659.
Diagnostic features (Figs 43 L, M): Males 8.9–10.3 mm; females 10.4–11.7 mm; lips inflated, highly sculptured; four interlabia present; cephalic setae elongate; buccal capsule unstriated; flap-like valves absent at base of buccal capsule; spicules 1.51–1.75 mm; female tail short, conical, 0.26–0.38 mm; ovejector J-shaped.
Comments: This species is known only from *Dend. lumholtzi* from north-eastern Queensland.

***Zoniolaimus elegans* Beveridge, 1983**

Zoniolaimus elegans Beveridge, 1983, pp. 21–23, figs 27–35, 224; Beveridge et al., 1998, p. 481.

Type data: holotype SAM V2945, allotype SAM V2946, paratypes SAM V2947–2956, BMNH 1981.3678–3679, USNPC 76626.
Type locality: Rivertree, NSW (28° 39′S 152° 18′E).
Type host: *Notamacropus parryi* (Bennett, 1835).
Site in host: stomach.
Distribution: eastern Qld, north-eastern NSW.
Representative DNA sequence data: ITS1, 2: MG 865660.
Diagnostic features (Figs 43 J, K): Males 6.9–9.7 mm; females 9.2–11.7 mm; lips flap-like, inornate; interlabia absent; cephalic setae elongate; buccal capsule unstriated; flap-like valves present at base of buccal capsule; spicules 2.27–2.69 mm; female tail elongate, 0.63–0.92 mm long; ovejector J-shaped.
Comments: This species is common in *N. parry* in Queensland (Beveridge et al., 1998).

***Zoniolaimus latebrosus* Huby-Chilton, Beveridge, Gasser & Chilton, 2002**

Zoniolaimus latebrosus Huby-Chilton, Beveridge, Gasser & Chilton, 2002, pp. 140–142, figs 12–24; Beveridge, 2020c, p. 4, 2020e, p. 204.

Type data: holotype SAM AHC 31381, allotype SAM AHC 31382, paratypes SAM AHC 31383.
Type locality: Calooma Station, 50 km N of Bourke, NSW (29° 39′S 145° 54′E).
Type host: *Osphranter rufus* (Desmarest, 1822).

Other hosts: *Macropus fuliginosus* (Desmarest, 1817), *M. giganteus* Shaw, 1790; *Osphranter robustus* (Gould, 1840).

Site in host: stomach.

Geographical distribution: Qld, NSW.

Representative DNA sequence data: ITS1, 2: KJ776404, KJ 851996–852000.

Diagnostic features (Figs 43 D, E): Males 6.8–9.1 mm; lips flap-like, inornate; 4 interlabia present; cephalic setae elongate; buccal capsule unstriated; flap-like valves present at base of buccal capsule; spicules 1.53–1.95 mm; female tail elongate, 0.65–0.78 mm long; vagina elongate 1.47–1.75 mm; ovejector J-shaped.

Comments: This species was formerly confused with *Z. mawsonae* with which it may co-occur. It is most easily distinguished from *Z. mawsonae* by spicule lengths (0.94–1.23 mm in *Z. mawsonae*, 1.53–1.95 mm in *Z. latebrosus*) and the shape of the female tail, which is swollen in the region of the vulva in *Z. mawsonae*, but not in *Z. latebrosus*. The principal host of *Z. latebrosus* is *O. rufus*, with additional records from other hosts (Spratt & Beveridge, 2016; Beveridge, 2020) representing uncommon findings.

***Zoniolaimus mawsonae* Beveridge, 1983**

Zoniolaimus mawsonae Beveridge, 1983, pp. 17–18, figs 10–17; Beveridge et al., 1992, p. 365; Beveridge et al., 1998, p. 481; Huby-Chilton et al., 2002, pp. 138–140, figs 1–11; Beveridge, 2020c, p. 4; 2020e, p. 204.

Type data: holotype SAM V2933, allotype SAM V2934, paratypes SAM V2935–2944, BMNH 1981.3676–3677, USNPC 76625.

Type locality: Cunnamulla, Qld (28° 04′S 145° 41′E).

Type host: *Osphranter rufus* (Desmarest, 1822).

Other hosts: *Onychogalea unguifera* (Gould, 1840); *Osphranter robustus* (Gould, 1840).

Distribution: Qld, NSW.

Representative DNA sequence data: ITS1, 2: MG 865661.

Diagnostic features (Figs 43 A–C): Males 7.4–10.2 mm; lips flap-like, inornate; 4 interlabia present; cephalic setae elongate; buccal capsule unstriated; flap-like valves present at base of buccal capsule; spicules 0.94–1.23 mm; female tail swollen in region of vulva, 0.52–0.68 mm long; vagina short 0.41–0.55 mm; ovejector J-shaped.

Comments: The principal host of this species is *O. rufus*, with additional records from other hosts (Spratt & Beveridge, 2016; Beveridge, 2020) representing uncommon findings. Differentiation from the co-occurring species, *Z. latebrosus*, has been described above.

***Zoniolaimus niuginiensis* Beveridge, 1983**

Zoniolaimus niuginiensis Beveridge, 1983, pp. 26–27, figs 60–69; Flannery et al., 1996, p. 187.

Type data: holotype, BMNH 1981.3724, allotype BMNH 1981.3725, paratypes BMNH 1981.3726–3762.

Type locality: Lake Trist, Papua New Guinea (7° 30′S 146° 57′E).

Type host: *Dendrolagus goodfellowi* Thomas,1908.

Other hosts: *Dendrolagus dorianus* Ramsay, 1883; *D. inustus* Müller, 1840; *D. matschiei* Forster & Rothschild,1907; *D. mbaiso* Flannery, Boeadi & Szalay, 1995; *D. scottae* Flannery & Seri, 1990.

Site in host: stomach.

Distribution: PNG.

Diagnostic features (Figs 43 N, O): Males 7.8–10.3 mm; females 8.7–11.1 mm; lips inflated, sculptured; interlabia absent; cephalic setae short; buccal capsule faintly striated; flap-like valves absent at base of buccal capsule; spicules 1.76 – 1.99 mm; female tail elongate, conical, 0.39–0.55 mm; ovejector J-shaped.

***Zoniolaimus occidentalis* Beveridge, 1983**

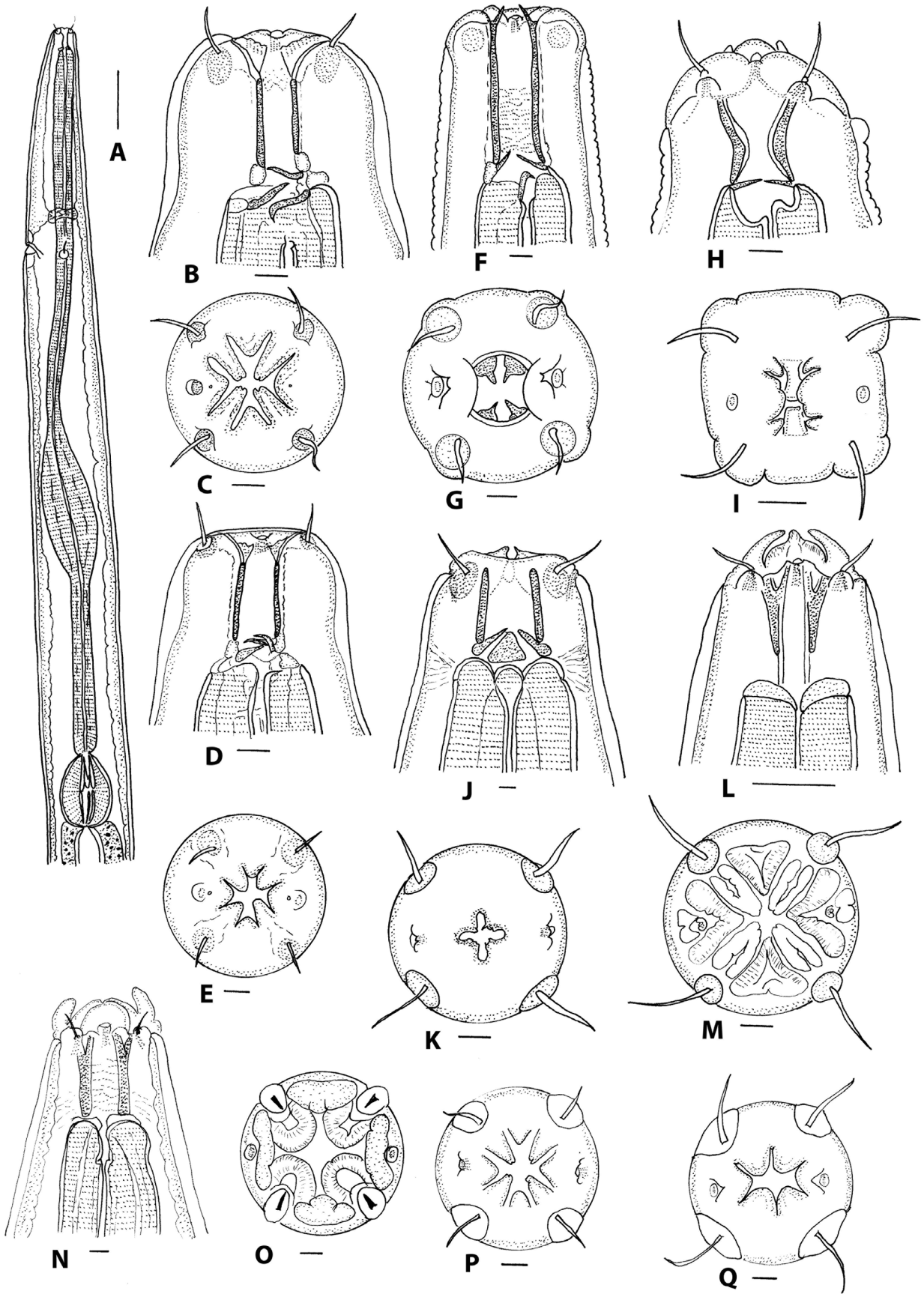
Zoniolaimus occidentalis Beveridge, 1983, pp. 27–29, figs 70–82.

Type data: holotype SAM V2969, allotype SAM V2970, paratypes SAM V2971–2974, AHC 11332, BMNH 1981.3682–3683, USNPC 76628.

Type locality: 50 km south-east of Perth, WA (32° 24′S 116° 18′E).

Fig. 43. Genus *Zoniolaimus*. A, *Zoniolaimus mawsonae*, anterior end, lateral view; B, *Z. mawsonae,* buccal capsule, lateral view; C, *Z. mawsonae*, anterior end, apical view; D, *Zoniolaimus latebrosus,* buccal capsule, lateral view; E, *Z. latebrosus,* anterior end, apical view; F, *Zoniolaimus petrogale,* buccal capsule, lateral view; G, *Z. petrogale,* anterior end, apical view; H, *Zoniolaimus occidentalis*, buccal capsule, lateral view; I, *Z. occidentalis,* anterior end, apical view; J, *Zoniolaimus elegans*, buccal capsule, lateral view; K, *Z. elegans,* anterior end, apical view; L, *Zoniolaimus dendrolagi*, buccal capsule, lateral view; M, *Z. dendrolagi,* anterior end, apical view; N, *Zoniolaimus niuguiniensis*, buccal capsule, lateral view; O, *Z. niuguiniensis,* anterior end, apical view; P, *Zoniolaimus setifera,* anterior end, apical view; Q, *Zoniolaimus buccalis,* anterior end, apical view. (A–E from Huby-Chilton et al, 2002; F–Q from Beveridge, 1983).

Scale-bars: A. 0.1 mm; B–Q, 0.01 mm.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Type host: *Notamacropus irma* (Jourdan, 1837).
Site in host: stomach.
Distribution: south-western WA.
Representative DNA sequence data: ITS1, 2: OM987392 (unpublished, voucher specimen SAM AHC 48462).
Diagnostic features (Figs 43 H, I): Males 6.2–6.9 mm; females 5.9–7.6 mm; lips flap-like, inornate; 2 lateral interlabia present; cephalic setae elongate; buccal capsule unstriated, sinuous in lateral view; flap-like projections in mid-region of buccal capsule; flap-like valves present at base of buccal capsule; spicules 1.36–1.62 mm; female tail slender, 0.29–0.41 mm long; vagina short 0.65–0.85 mm; ovejector J-shaped.
Comments: This distinctive species differs from congeners in the features of the lips and buccal capsule. It appears to be limited to *N. irma* in the south–west of Western Australia.

***Zoniolaimus petrogale* Beveridge, 1983**

Zoniolaimus petrogale Beveridge, 1983, pp. 23–24, figs 36–47; Begg et al., 1995, p. 47; Beveridge et al., 1989, p. 277.
Type data: holotype SAM V2975, allotype SAM V2976, paratypes SAM V2977–2980, AHC 11330, BMNH 1981.3684–3685, USNPC 76629.
Type locality: Proserpine, Qld (20° 24'S 148° 35'E).
Type host: *Petrogale persephone* Maynes, 1982.
Other hosts: *Petrogale godmani* Thomas, 1923.
Site in host: stomach.
Distribution: north-eastern Qld.
Representative DNA sequence data: ITS1, 2: MG 865662.
Diagnostic features (Figs 43 F, G): Males 7.8–9.3 mm; females 9.5–11.6 mm; lips flap-like, inornate; interlabia absent; labial supports project beyond labia; cephalic setae elongate; buccal capsule faintly striated, cylindrical in lateral view, quadrangular in transverse section; flap-like valves present at base of buccal capsule; spicules 1.76–2.21 mm; female tail slender, 0.43–0.64 mm long; vagina elongate 0.80–1.05 mm; ovejector J-shaped.
Comments: This species is primarily parasitic in *Pet. persephone* with a limited occurrence in the related rock wallaby *Pet. godmani*.

***Zoniolaimus setifera* Cobb, 1898**

*Zoniolaimus setife*ra Cobb, 1898, p. 312, fig. 30; Railliet & Henry, 1913, p. 506; Baylis & Daubney, 1926, p. 163; Yorke & Maplestone, 1926, p. 176; Johnston & Mawson, 1939b, pp. 520–521, figs 19–22; Kung, 1948, pp. 104–107; Skrjabin et al, 1952, p. 172, fig. 85; Popova, 1960, pp. 71–72, fig. 43; Yamaguti, 1961, p. 403; Beveridge, 1983, pp. 14–16, figs 1–9, 218; Spratt et al., 2017, p.241.
Type data: unknown.
Type locality: Moss Vale, NSW (34° 33'S 150° 23'E).
Type host: *Notamacropus rufogriseus* (Desmarest, 1817).
Site in host: stomach.
Distribution: eastern Qld, eastern NSW.
Representative DNA sequence data: ITS1, 2: MG 865663.
Diagnostic features (Fig. 43 P): Males 3.8–6.3 mm; females 5.0–6.9 mm; lips flap-like, inornate; lateral, dorsal and ventral interlabia present; cephalic setae elongate; buccal capsule unstriated; flap-like valves present at base of buccal capsule; spicules 1.11–1.31 mm; gubernaculum absent; female tail elongate, 0.40–0.53 mm long; ovejector J-shaped.
Comments: This species is common in *N. rufogriseus* in eastern Australia, but has not been found in the same host species in western Victoria and Tasmania (Aussay et al., 2011; Vendl & Beveridge, 2014; unpublished observations).

* * * *

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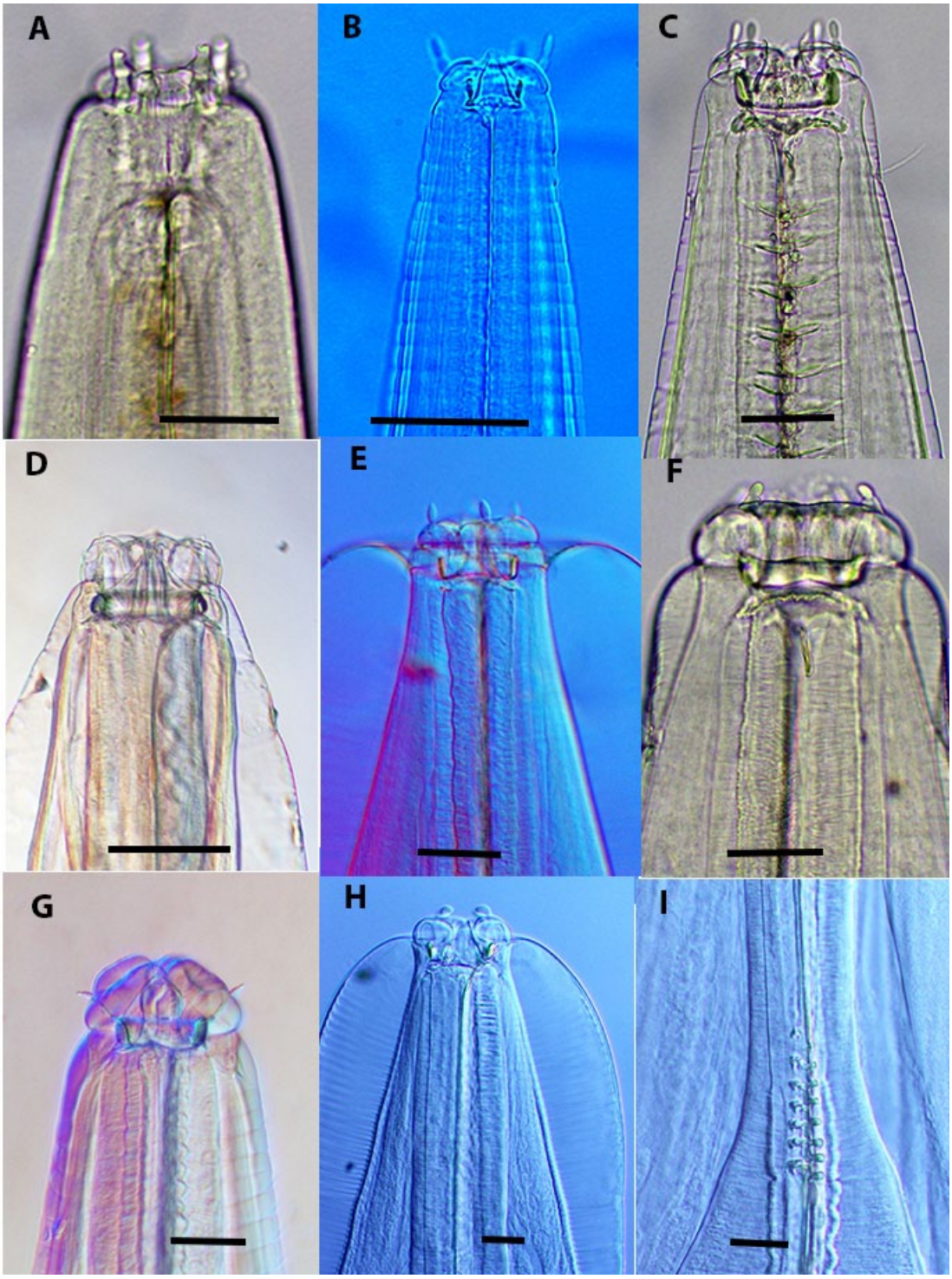

Fig. 44. Photomicrographs of the buccal and oesophageal regions of selected cloacinine species. A, *Alocostoma clelandi*; B, *Cloacina brazellei*; C, *C. communis*; D, *C. dahli*; E, *C. expansa*; F, *C. frequens*; G, *C. parva*; H, *C. themis*; I, *C. themis*, oesophageal denticles.

Scale-bars: 0.05 mm.

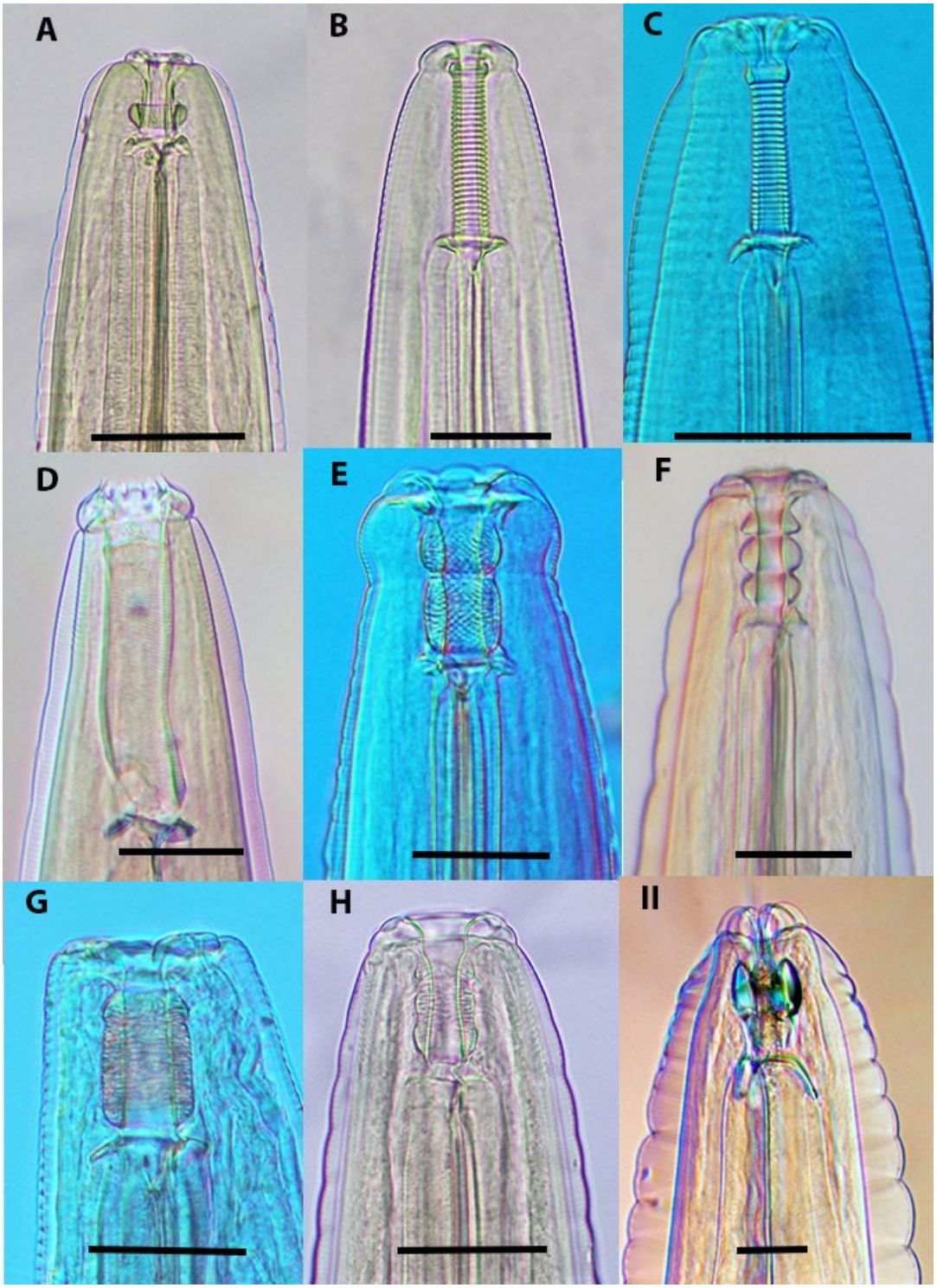

Fig. 45. Photomicrographs of the buccal regions of selected cloacinine species. A, *Coronostrongylus coronatus*; B, *Cyclostrongylus alatus*; C, *Pararugopharynx protemnodontis*; D, *Pharyngostrongylus thylogale*; E, *Rugopharynx epsilon*; F, *R. sigma*; G, *R. spratti*; H, *R. zeta*; I, *Thylonema thylonema*.

Scale-bars: 0.05 mm.

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